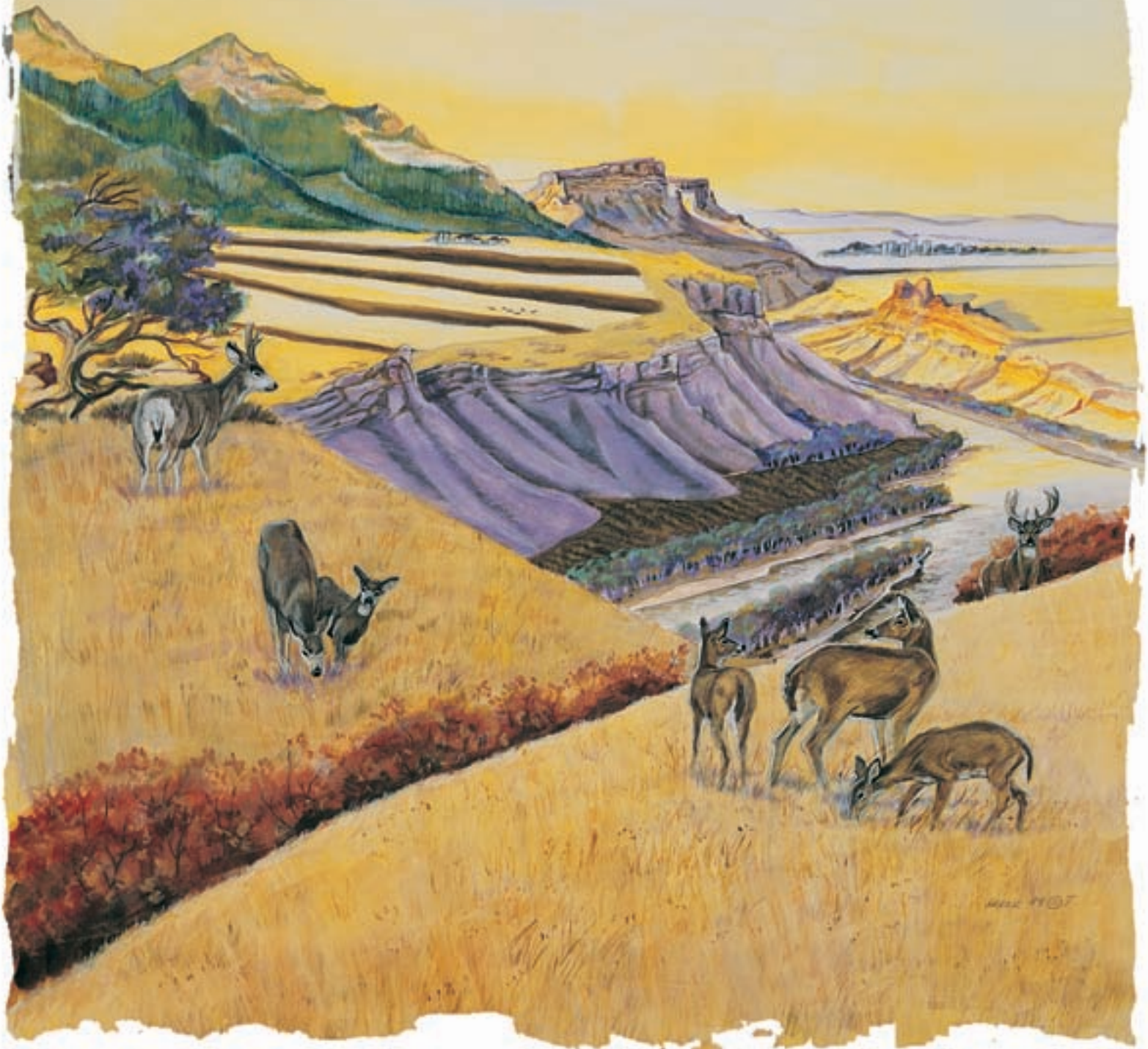# ECOLOGY AND MANAGEMENT
of Mule Deer and White-tailed Deer
in Montana

Ecology and Management of Mule Deer and White-tailed Deer in Montana

By

Richard J. Mackie, David F. Pac,
Kenneth L. Hamlin, and Gary L. Dusek

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Foreword

Mule deer and white-tailed deer are the most widely distributed and abundant big game mammals in Montana. Although evolved to live and thrive in broadly different environments, the two species are remarkably adaptive. Both occur in a wide variety of habitats, under widely fluctuating environmental conditions, in the presence of numerous other wild mammals and domestic livestock, and in the wake of extensive human development and disturbance.

Managing deer across diverse habitats and conditions in Montana begins with understanding both their biology and behavior. It also requires effective methods for monitoring populations and habitats as well as for manipulating deer numbers or habitat factors to meet diverse social and economic objectives.

Montana has a long history of research to provide basic information about deer and their habitats and to develop and test new and improved methods and criteria for deer management. Studies during the 1940s and '50s provided most of the first scientific data, laying the foundation for "deer management based on facts." Later, studies evaluated and refined some of the early management concepts and methods and their applications.

By the early 1970s, the environments in which deer existed were changing rapidly. Some methods for deer management became outdated and it was evident that new information and approaches were necessary. In 1975, an important long-term and comprehensive statewide research effort was initiated employing new and emerging technologies in research on both species and across a broad spectrum of environments in Montana. Numerous ancillary studies mostly in the form of 2-year graduate student research projects were conducted in association with this long-term investigation.

This bulletin was prepared as a comprehensive summary of results from all of these studies. Like earlier efforts, the results lend additional insight to understanding the behavior, biology and ecology of the two species. However, unlike earlier investigations, this investigation focused on formulating research results into management recommendations. This resulted in important advances to refine management strategies and practices to help reduce some of the uncertainty that always exists in dealing with wildlife resources in complex environments.

Donald A. Childress
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Preface

The research presented in this report was funded and sponsored by hunters and the Federal Aid in Wildlife Restoration program. Together they have provided major funding for scientific game management since 1941, including numerous short-term and comprehensive long-term field research investigations as reported in this bulletin. Although the information presented herein is definitive, no reader should be deluded into thinking these are the "last words" in our understanding of Montana's two most numerous large mammals. Our knowledge can never be complete, nor will management be conducted with certainty. As the environment and society changes, so must our knowledge of deer-habitat relationships. Research is one means of obtaining the wherewithal to recognize and adapt management to those changes.

It is difficult to consider deer separate from their environment. All that deer are and all that deer do are biological and behavioral responses to the environments in which they occur as individuals, populations, and species. This bulletin expands on that view in discussions of deer-habitat relations and deer population ecology. For example, the term "habitat" has been defined and characterized by many but understood by few. Ask anyone what constitutes "deer habitat" and most will describe a landscape that usually includes a buck and/or a doe, and often a fawn or two in a picturesque outdoor setting. Such images are designed for economic markets or artwork and not scientific understanding. Only when the "concept" of habitat is described in terms of juxtaposition of all components and their use by individual deer or family units of deer, does habitat become truly meaningful. Deer habitat is multidimensional and must include not only the basic components for survival, but also the social behavior of deer.

Individual deer of both sexes comprise the basis of a deer population. However, partitioning environments into deer matriarchal units surrounded by nearby and overlapping younger female units is integral to understanding both how populations operate and for management options of the two species. Male habitat selection and survival, while necessary for species continuance, is peripheral to the importance of matriarchal units for maintenance or increases in deer populations. Females establish the ultimate pattern of deer population distribution in both new habitats and in habitats recolonized after population declines.

Understanding population characteristics and dynamics, including age structure of the female segment and patterns and rates of fawn recruitment and adult mortality, are crucial to managing deer at the local level. The severe reduction or loss of one cohort due to environmental stress often linked with predation may not be critical to the population, but severe reductions in two or more consecutive cohorts can set the stage for a significant population decline. Conversely, good survival of consecutive cohorts can foretell an imminent population increase.

The probability of survival is high for most deer after achieving adulthood. The majority of adult deer mortality can be accounted for by legal hunting, terminal wounding losses and illegal killing. This human-induced mortality replaces some natural mortality in adults, but those latter rates are normally quite low. However, occasional episodes of high natural mortality of adult females also can trigger population declines, especially in association with low fawn recruitment.

The authors have emphasized the importance of behavior in habitat relationships and population dynamics. Social behavior, while hard to quantify and explain, is often the driving force in selection of certain habitats and avoidance of other habitats. It also is an important element that allows local subpopulations to use habitat most efficiently, at optimal densities, and adapt to fluctuations and other changes in the environments deer occupy.

Land use changes and hunting regulations over the last two decades have led to a dramatic increase in distribution and abundance of white-tailed deer in Montana (In 1996, and for the first time on record, the statewide white-tailed deer harvest was higher than the mule deer harvest). This in turn has led to a significant overlap in the distribution of the two species. Despite this overlap and parallel strategies for habitat selection, they remain two distinctly separate species that typically select and use very different habitats within their range. Just as our knowledge about mule deer and white-tailed deer has evolved, so too must our philosophy about managing them as separate species as distinct from one another as either is from elk or antelope, for example.

Humans are an integral part of the ecology of deer. Their greatest long-term impacts are on deer habitat (good and bad). In effect a major predator, they are responsible for a significant amount of annual mortality of deer through hunting and other means. Although hunter harvests of deer have been monitored

for almost 50 years, only in the past decade or so have biologists begun to define, quantify, and understand the interaction of all causes of mortality in population ecology.

In terms of management, the results herein indicate that many existing theories or "principles of deer management" are less applicable than commonly believed. Traditional interpretation of "carrying capacity" did not explain observed deer-habitat interactions on or among the various study areas. The concept of a consistent "limiting factor" influencing deer population dynamics statewide could not be identified. Similarly, the concept of "compensatory" increases in fawn recruitment and deer numbers or decreases in natural mortality with increased hunter harvests and reduced population density was discussed as having limited application. To assume the general existence and operation of these concepts in population dynamics of both species, across all environments, and over time will likely result in misinterpretation of management opportunities.

Harvest rate recommendations presented in this bulletin, if based on the required information, may cause some concern among law enforcement personnel and the public. Why? Because harvest regulations for deer populations existing in close proximity may be subject to different population control strategies. It may take considerable time for hunters and the public to realize that populations or other groups of deer in close proximity to one another may not be influenced by the same land management practices, hunting influences, and environmental factors (in fact what is bad or has negative effects in one place or at one time may be good or beneficial in another). Recognizing this and applying it to harvesting and overall management of deer may complicate rather than simplify hunting regulations and assessment of environmental impacts. Monitoring deer numbers and harvests and their respective compositions will require time

and appropriate procedures along with administrative and political support. The less this occurs, the more speculative the recommendations for hunting seasons, and the lower the probability of successfully achieving long-term deer management goals and objectives.
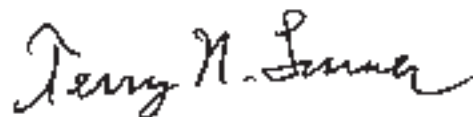
Management of deer at virtually any population level may be possible in many areas once desired deer numbers, density, and population-units are delineated. Because of the vagaries of weather, however, population goals should fall within numerical ranges, not point estimates, based on observed or reasonably expected values for population fluctuations in a given environment over time. Other important components in designing deer management goals include agricultural and forest economics, land development activities, traffic safety, and social tolerances for hunters, hunting, and wildlife viewers.

Biologists, hunters, landowners and the general public have experienced two "reality checks" in deer management in Montana during the past 25 years:

the first during 1972-1977, the second beginning in 1995. The reaction to the next "check" will reflect our knowledge, skills and ability to detect population fluctuations and respond with appropriate adjustments in hunting regulations.

The research results and management implications presented in this bulletin provide some new information about modeling the effects of size (numbers of animals) and density (number of animals per unit area) as separate but interactive population parameters. Based on biological parameters and ecological boundaries, these models allow managers to test the impacts of various mortality factors, including harvest strategies, on existing deer populations and future trends.

Another deer decline will doubtless occur early in the 21st Century, but if the management regimes presented in this bulletin are accepted and implemented, fluctuations may be better predicted and receive more timely management responses.

Terry N. Lonner

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Chief, Research and Technical Services
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New paradigms will replace old when the new can explain anomalies between observation and the old paradigms.

Kuhn 1970

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Historical Perspective

Deer management in Montana has traditionally attempted to satisfy the requirements of deer for survival and provide maximum hunting opportunity. Beginning in the 1940s, management was based on a conceptual model in which the key elements were winter range, the quantity and quality of forage (i.e., browse) available on primary wintering areas, and deer numbers and distribution relative to these resources.

This model was developed from early knowledge of deer biology and theories about population ecology. It assumed that deer populations were highly productive, inherently irruptive, and capable of overpopulating and overbrowsing their ranges unless controlled by hunter harvest. Forage, particularly the winter browse supply, was assumed to be the primary factor limiting populations. "Carrying capacity" was the number of deer a range could sustain in balance with the forage supply. As deer numbers reached or exceeded carrying capacity, the amount and quality of winter browse available to individual deer declined, resulting in widespread malnutrition and death from starvation. Malnutrition also adversely affected reproduction, body size, and antler growth.

It also was assumed that heavy browsing had another, perhaps even more insidious, effect. Overuse of important plants resulted in a hedged appearance; browse plants declined in size and productivity until they died and were replaced by less nutritious and palatable plants. In this manner, carrying capacity presumably could be reduced to the point where the range would support fewer deer. Deer browsing was the primary factor affecting forage plant abundance and productivity and deer could degrade their own habitat.

Based on these concepts, many biologists defined deer habitat synonymously with the browse supply on winter range. Healthy, productive winter forage produced healthy productive deer populations, and the way to sustain both was through sufficient hunter harvest to maintain the most favorable balance between population size and the "habitat."

Early concepts identified other potential limiting factors like predation, disease, parasites, and severe weather that could limit deer numbers. However, their effect was considered more an expression of an underlying nutritional problem that weakened and predisposed deer to those factors rather than direct limitation.

Regulated human predation, or hunting, was not considered limiting

Forage, particularly the winter browse supply, was assumed to be the primary factor limiting populations.

because it was not believed additive to other mortality. Instead, hunting mortality was believed to be "compensatory", i.e., it replaced natural mortality which would otherwise occur. It also reduced population density to promote increased survival and reproduction among remaining deer.

Within this conceptual framework, deer were "deer," i.e., mule deer, white-tailed deer, bucks and does, adults and young, were essentially the same organisms from a management perspective. Hunting and harvest were the primary tools for both population and habitat management as well as the primary measure of success in deer management. The task of managers was to develop harvest strategies and sustain sufficient hunter harvests to maintain healthy, productive forage and deer populations on winter range.

The framework also simplified management because biologists could focus surveys on a small portion (usually <20 percent) of the total yearlong range of deer. Further, an elusive and controversial estimate of the total numbers of deer on a range or in a population was not necessary. One needed only measure utilization and condition of "key" browse plants on "key" winter range areas to determine whether deer populations were too high, about right, or too low in relation to carrying capacity. Other databases (such as trend in number of deer harvested and fawn production), which were assumed to be directly related to utilization and condition of winter browse, also could be sampled with reasonable ease and accuracy.

By the 1940s and early 1950s, concurrent with these developing concepts, deer populations were expanding almost explosively. Restrictive hunting seasons severely limited deer harvests locally and statewide. Major predators (wolves, mountain lions, and coyotes) had been reduced or eliminated from their natural ranges in Montana. Favorable habitat conditions developed in association with the end of the 1930s drought. Changes in livestock grazing,

Regulated human predation or hunting was not considered limiting because it was not believed additive to other mortality. Instead, hunting mortality was believed to be "compensatory"

agriculture, and logging provided increased habitat diversity and high energy forage for deer. In some areas of eastern Montana, dwindling human populations reduced disturbance and restored natural habitat.

Growing deer populations brought new, unprecedented problems and conflicts. The first three decades of the century witnessed low deer numbers and development of a protectionist mindset among hunters and landowners. By the early 1950s, "overabundance" and depredations on agricultural, range, and forest lands brought need for expanded harvests for population control. To conservation-minded sportsmen, however, the notion of liberalizing hunting regulations from bucks-only to either sex or doe seasons was unthinkable. Thus, the new "management model," though offering increased opportunity for recreational hunting and greater hunting-harvest success, faced formidable social barriers.

Theory and practice embodied in this winter forage limiting model provided biologists with an objective, scientific basis to address the problems of overabundance. It also gave new opportunities for management.

Few wildlife management programs have been pursued as aggressively or implemented so widely as " deer management based on facts" (Cole 1958, 1959, 1961; Newby 1958). The history and results of the program from the early 1950s through the early 1970s are documented in deer hunting regulations and harvest records maintained since 1945, as well as in reviews of deer management from 1941 through 1970 by Allen (1971) and Egan (1971).

Efforts to expand hunting opportunity and reduce burgeoning deer populations through special either sex or "doe" hunting seasons began in western Montana in 1951 and 1952. Five years later, almost the entire state was opened to general hunting of two deer of either species, either sex, during a one-month season. In addition, nonresident hunting was expanded by offering $20 either-sex permits in many hunting districts. Areas

with severe overbrowsing or agricultural depredations were frequently delineated for special early or late seasons allowing harvest of additional antlerless animals.

Under this management strategy, which represented an intensive statewide effort to apply "sustained yield harvest theory" to deer populations in Montana, harvests increased from less than 40,000 deer annually prior to 1952 to over 100,000 by 1955. Annual harvests exceeding 100,000 deer were sustained into the early 1970s with few exceptions. During much of this period, antlerless deer constituted 25 to 40 percent of the statewide harvest. By conservative estimate, total legal harvests probably removed no less than 10 percent of autumn populations statewide (a statewide harvest of 100,000 deer would, at 10 percent, require an average density of about 3 deer per square kilometer across the entire state, or an average of 4/km^2 on two-thirds of all land in the state). Check station data and statewide harvest survey estimates for individual hunting districts indicated much higher than average harvest rates occurred locally, especially in areas of special management concern.

Unfortunately, this aggressive practice of deer management through liberal hunting seasons did not sustain deer populations or harvests. Change was on the way as mule deer numbers began to decline in Montana and across much of western North America during the late 1960s and early 1970s.

As early as the mid-1960s, biologists and others began questioning some of the concepts and practices that were broadly applied when deer were extremely abundant. Some questioned the effectiveness of range survey methods and criteria for interpreting deer range conditions. Others believed that not enough deer were killed to achieve a balance between deer populations and available range. As a result, new studies were requested to provide an ecological basis for determining range condition and trend in the statewide management program and to determine the degree of harvest necessary to maintain the balance

where ranges had deteriorated and deer numbers had declined. Yet, few deer managers were skeptical of the simple, cause-effect relationship between deer and their habitat.

Research initiated in 1970 to evaluate range surveys confirmed numerous technical, analytical, and conceptual problems with the program. Range survey data had only limited utility in expressing real trends in plant utilization and condition; in many cases they were inaccurate (Mackie 1975). The findings also raised questions about the general applicability of basic concepts about deer-habitat interactions; especially the simple, direct relationship between deer populations and the supply and condition of key browse plants on key winter ranges.

Where data were available, browse utilization and condition trends were not related to deer population trends. Winter browse supply was only one of many factors influencing deer populations, and deer use was but one of many factors influencing plant populations and forage supplies (Mackie 1973, 1975). Winter concentrations of deer and heavy use of browse probably revealed only where deer ended up and what they subsisted on under desperate conditions (Carpenter and Wallmo 1981). Winter concentrations were not indicative of an overriding importance of winter relative to other seasonal ranges.

Under this management strategy, which probably represents the best statewide effort ever attempted to apply "sustained yield harvest theory" to deer populations, Montana deer harvests increased from less than 40,000 deer annually prior to 1952 to over 100,000 by 1955.

Widespread declines in mule deer populations during the early-mid 1970s came as a shock to most biologists. Theoretical concepts and principles of deer management could not explain the decline (MCTWS 1975, Workman and Low 1976). Pengelly (1976) indicated that the effects of nearly all limiting factors including hunting on deer populations were poorly understood. Specific findings concerning limiting factors were confusing or contradictory.

Deer science lacked a broad, long-term population perspective that included importance of the interaction among factors. Most deer management principles were derived from short-term studies on a few problem areas at a time when deer populations were abundant or from controlled experiments in pens. Basic theory and management concepts about population ecology and sustained yield harvest were largely untested.

Statewide Deer Research Studies

Studies on deer in Montana during the 1950s and 1960s were designed primarily to identify problems and provide information on food habits and winter range use. A few evaluated the efficacy of management programs and concepts, as in the case of browse surveys. However, these studies were not sufficient to explain deer population phenomena nor to answer concerns about existing management theory and practices.

Because of this, comprehensive studies on the population ecology of both species in representative Rocky Mountain and Great Plains habitats were initiated during 1975. Established upon a base of earlier deer research, the new studies were designed to:

- provide more detailed knowledge and an improved understanding of the biology and population ecology of mule deer and white-tailed deer in Montana
- develop new or improved methods for managing mule deer and white-tailed deer populations and habitats, and
- establish new guidelines for consideration of mule and white-tailed deer in other wildlife, range, forest, and land management programs.

A long-term, comparative evaluation of deer-habitat interactions and population ecology among species and environments would provide basic knowledge about deer and insight to important management questions. For example:

- what constitutes deer habitat?
- how do deer select and use habitat and adapt to habitat variation?
- what constitutes habitat condition/ habitat quality?
- how can condition trends be measured effectively?
- what constitutes a deer "population"?
- how are populations organized and maintained over time?
- how do populations vary in space and time?
- how does the interaction of natural mortality and hunting influence population dynamics?

The research embraced spatial and temporal scales previously avoided in studies on deer. Included were six intensive investigations in the major ecological types occupied by deer in Montana (Fig. 1). All were full-time field studies conducted concurrently for periods ranging from 7 to more than 20 years. Additional, comparative data were available from earlier research and numerous less intensive, shorter term studies throughout the state.
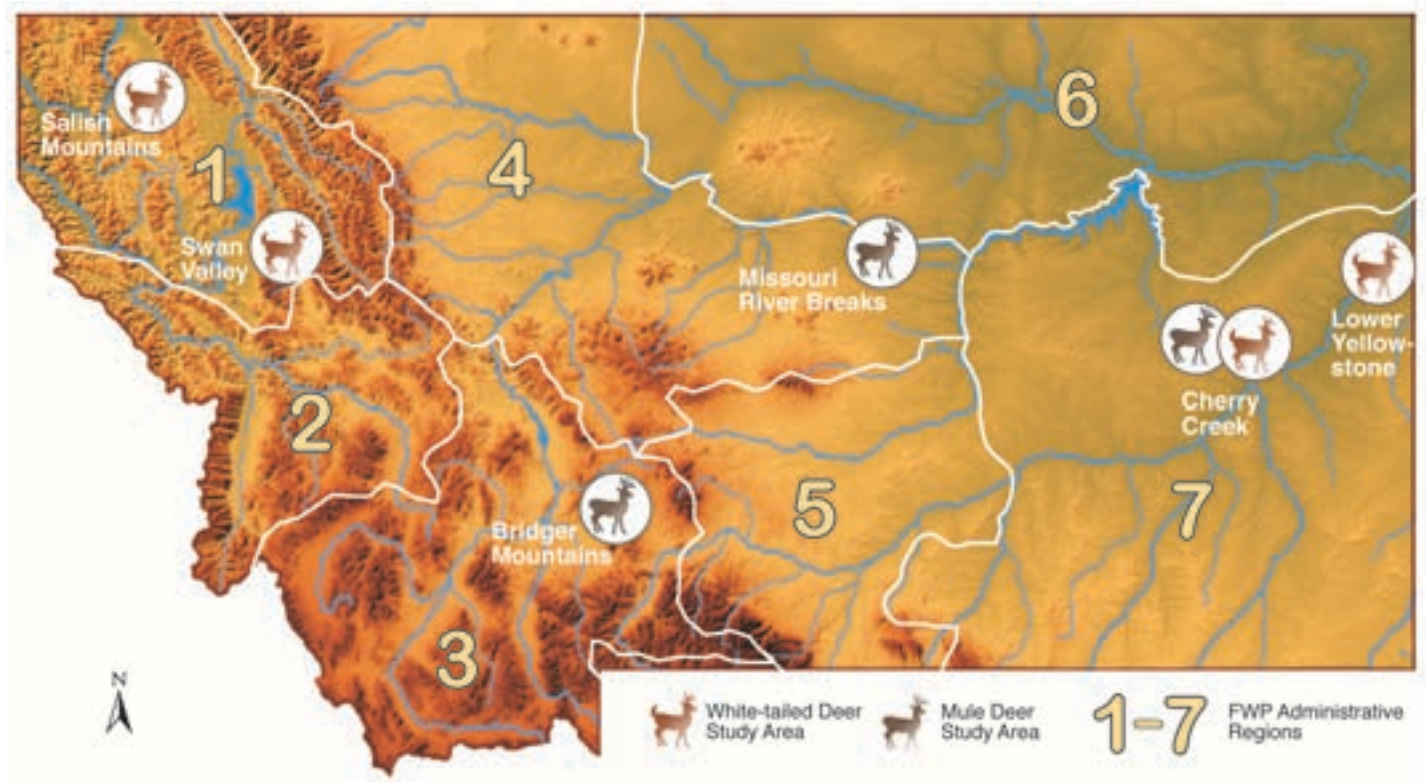
Figure 1.
Locations of major deer study areas and boundaries of Montana Fish, Wildlife and Parks administrative regions.

Methods

Similar methods were employed on all areas, though some were modified in accord with local logistical constraints and individual study objectives. Technology available for field investigation and data analysis changed markedly through time, and we upgraded our methods during the work.

On each of the primary study areas we endeavored to define:

- characteristics of the habitat in terms of physical and biotic attributes
- deer behavior or use of the area (distribution, movements, home range size and shape, use and selection for vegetation/cover types, activity patterns, and food habits)
- biological attributes of deer (growth patterns, body size, condition, longevity, reproduction, and mortality)
- deer population characteristics (size, sex and age structure) and dynamics (annual recruitment and adult mortality rates, immigration, and emigration) over time and across the range of environmental variation that occurred.

Details of methods used are given in final reports and publications for each of the studies (e.g., Dusek *et al.* 1989, Wood *et al.* 1989, Hamlin and Mackie 1989, Pac *et al.* 1991). Only a broad overview is presented here.

All study areas were described in terms of geographic location, topography, climate and weather, vegetation, major fauna, and land uses. Environmental descriptions, the system or intensity of mapping, and mode of analysis varied among studies and over time. For example, after studies in the Bridger Mountains indicated that mule deer were distributed in seven, relatively discrete "population-habitat units," habitat investigations were redirected to comparative analysis of environmental features and patterns of variation within and among units. Also, early analyses were relatively simple and utilized very general measurements. Others completed later in the studies were more complex and utilized detailed databases generated by computers and GIS mapping technology.

All of the studies relied on radio-collared and other individually marked deer to define habitat relationships and assess population characteristics and dynamics. Deer were captured and marked with radio collars or neckbands using various techniques that included bait trapping in corral and Clover traps,

rocket netting, chemical immobilization, helicopter net gunning and drive netting, and hand capture of fawns. Collectively, we captured and marked approximately 2,500 mule deer and 1,600 white-tailed deer on the primary study areas from 1975 through 1995. Of these, 880 mule deer and 355 white-tailed deer were equipped with radio collars. Radio-collared individuals were relocated by periodic monitoring both from the ground and from the air; neck banded deer were observed as opportunities permitted. Most monitoring occurred during daylight hours, but triangulation at hourly intervals provided data on nighttime movements and activity over 24-hour periods in some areas. The development of highly reliable, long lasting radio transmitters enabled individuals and groups of deer to be monitored over several years. Some deer were recollared several times and followed for up to 13 years.

Intensive aerial surveys, employing fixed-wing aircraft and helicopters, also were used in determining habitat use and population characteristics and dynamics of deer in all areas except the densely forested whitetail habitats in northwestern Montana. Following procedures outlined by Mackie *et al.* (1981), Dusek *et al.* (1989), Wood *et al.* (1989), Hamlin and

Mackie (1989), and Pac *et al.* (1991), seasonal distributions and trends in population size and composition were determined over periods ranging from 7 to 35 years on major study areas.

Our use of complete-coverage surveys eliminated possible bias resulting from sampling design in population estimates. Flown by pilots and observers experienced in aerial deer surveys, the counts and classifications always represented the minimum numbers of deer and sex/age classes on study areas. To develop reasonable total population estimates, we had only to determine the accuracy of our counts. However, in most cases this approach precluded opportunity to calculate confidence limits around annual population estimates.

To account and adjust for visibility bias, we developed observability indexes (estimates of proportions of total deer observed) relative to study area/habitat, season, survey conditions, aircraft, and observer. These indexes, based on proportions of marked and radio-collared deer observed, were generally consistent from year to year within study areas and seasons when the same pilot and observer were used.

To further strengthen population estimates, data on population composition were applied in arithmetic
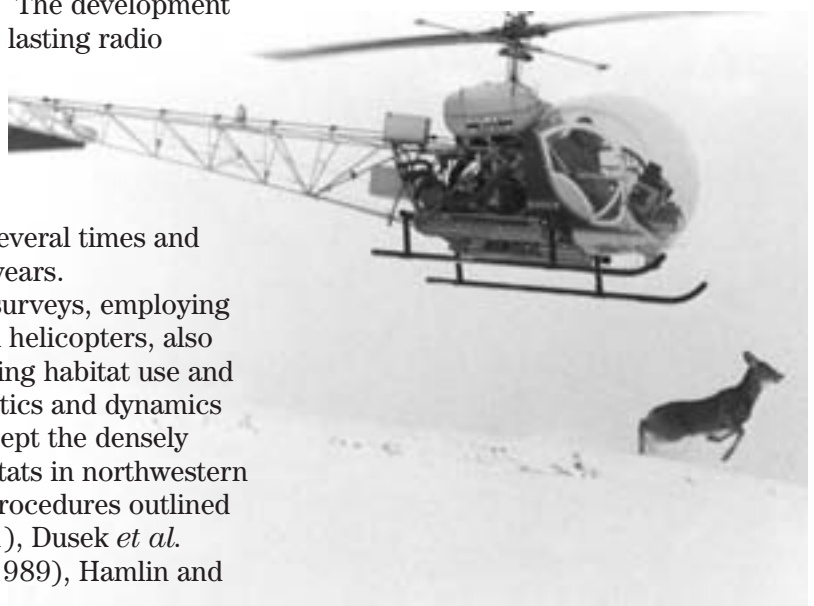
population models (Mackie *et al.* 1981) to reconcile any differences in estimates between seasons and years. Deer harvest and mortality patterns and rates among marked deer also were employed in modeling and confirmation of population estimates.

Ground surveys supplemented aerial surveys. They provided additional data on all study areas and provided the primary data on population characteristics and dynamics of white-tailed deer in densely forested northwestern Montana habitats. In recent years, camera surveys (Dusek and Mace 1991, Dusek and Morgan 1991) were also employed successfully to evaluate whitetail population parameters and habitat relationships in the Salish Mountains.

Deer harvest rates were estimated by marked and radio-collared deer. These data were corroborated by hunter check stations, field checks, questionnaires, and the Montana Fish, Wildlife and Parks' statewide deer harvest survey. Special dead-deer surveys were conducted on some areas during spring.

Sex, age, and various measurements were recorded for all deer captured, checked at stations, or examined in the field. Whenever possible, lower jaws or incisors were collected from deer examined at check stations or in the field. Ages were assigned in the field using tooth eruption and wear criteria (Severinghaus 1949, Robinette *et al.* 1957). When jaws or incisors were obtained, dental cementum analysis (Low and Cowan 1963, Gilbert 1966) also was employed to ascertain age. Weights, antler, and other measurements of biological characteristics and condition (Riney 1955, Greer 1968, Verme and Holland 1973) were also obtained. When possible, blood samples were collected from deer handled in traps or captured as fawns. During January-June, reproductive tracts were removed from any female mortalities to evaluate reproductive performance. Measurement of serum concentration of progesterone and pregnancy-specific protein B from peripheral blood (Wood *et al.* 1986) provided additional estimates for pregnancy rates. Rumen contents were sampled throughout the year for analysis of food habits.

Analytical procedures and methodology varied according to needs of individual studies. Statistical procedures generally followed Zar (1984). Most analyses were conducted using Montana State University computing services and a variety of computers, software, and statistical packages such as SAS (Ray 1982) and MSUSTAT (Lund 1983).

Environments Studied

Mountain-Foothill

Studies in the mountain-foothill environment centered in the Bridger Mountain Range. The Bridgers are a representative, semi-isolated range located at 45˚53' north latitude, 110˚53' west longitude, on the eastern flank of the Rocky Mountains in southwestern Montana (Fig. 1). Together with adjacent footslopes, the area encompasses about 2,000 km^2 and includes most of the topographic, climatic, and vegetational variation characteristic of mountain-foothill environments in Montana (Pac *et al.* 1991).

The Bridger Mountain Range is dominated by a north-south trending mountain divide that extends approximately 40 km in an arcuate pattern along the west flank. Three attending ridge formations extend easterly from the main divide to dominate the eastern flank and about two thirds of the total area. Elevations vary from 1,365-1,630 m along lower footslopes to 2,400-2,947 m along the main Bridger Range and 2,100-2,400 m at highest points along the eastern ridges. Overall, the west flank is characterized by high topographic relief and short, steep-sided drainages; the east flank is lower and less severe, with long drainages descending gradually through open benchlands, timbered foothills, and gently rolling footslopes.

The Bridger Mountains experience short, cool summers and long, cold winters, but local climates and weather patterns vary greatly. Average annual precipitation increases sharply with elevation from 40-45 cm along the western footslopes to an estimated 127 cm along the Bridger Divide, then declines progressively to the east and north to 35-40 cm.

In aspect, the Bridger Range and attending ridges and foothills comprise an "island" of montane forest within a "sea" of lowland steppe (Pac *et al.* 1991) (Fig. 2A). The steppe, dominated by open grass and shrub-grass communities, covers approximately 60 percent of the area. Montane forest, dominated by open to dense stands of several conifer species, covers 38 percent of the area within an elevational range of 1,830 m to 2,700 m. Highest elevations, above 2,400-2,700 m along the main Bridger Range divide, are characterized by a subalpine-alpine zone covering 2 percent of the total area.

Most of the Bridger Mountain study area, including nearly all of the steppe zone and about one-half of the foothill area, is privately owned. Lands above the lower limit of forest are predominantly in public ownership administered by the Gallatin National Forest. Along the east flank of the main Bridger Range ownership is in a checkerboard pattern with alternating sections of private timber lands. Grazing, dryland grain farming, hay production, timber harvest, and rural residential development are the primary uses of private lands. National forest lands are managed for timber harvest, livestock grazing, and recreation.

Early concerns about mule deer populations and damage to agricultural products led to a study of food habits, range use, and agricultural relationships on the west flank of the Bridger Range (Fig. 2B) during 1955-1956 (Wilkins

1957). This was followed by special studies to develop methods for deer range surveys during 1957-1959. During 1971-76, five graduate thesis projects and other special studies were conducted to further evaluate mule deer habitat relationships and range survey methods under the statewide range research project. All of these provided background and baseline data for further, long-term research on population ecology of mule deer beginning in 1975 (Pac *et al.*, 1991).

Figure 2. Mountain-foothill environment, the Bridger Mountains study area: looking north (A) and east across a major west slope winter range (B).
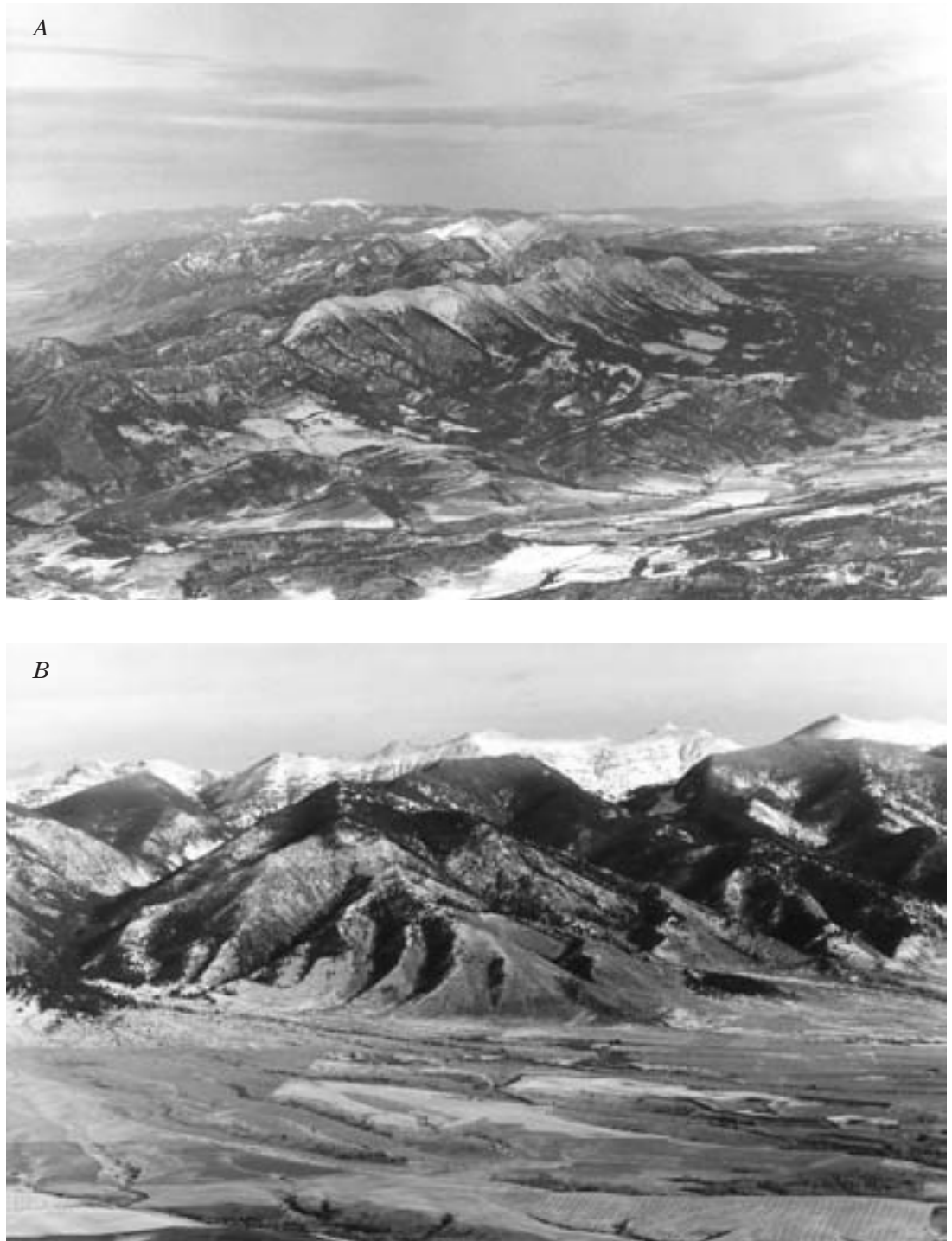
Timbered Breaks

Timbered breaks occur within a 10-50-km-wide by 300-km-long belt of rugged badlands along the Missouri River and its tributaries in northcentral Montana. The "breaks" are characterized by closely interspersed open ridges and sharply-cut drainageways or "coulees" that dissect the shale substrates of the area in a dendritic pattern and become progressively wider, deeper, and more steeply sloped as they approach the river.

Our studies centered on a representative 275 km^2 area located at 47˚ 30' north latitude, 108˚ 30' west longitude, about 40 km northeast of Roy in central Montana (Fig. 1). This area, described in detail by Mackie (1970) and Hamlin and Mackie (1989), extends about 30 km in a 7-11-km-wide band along the south side of the Missouri River. Elevations range from about 945 m on rolling plains along the southern edge of the area to about 685 m on the Missouri River floodplain.

The varied breaks topography and soils support a complex mosaic of open low shrub-grass and timbered vegetation types that impart a savannah-like aspect (Fig. 3A). Forested types cover about 50 percent of the area in scattered, open and medium density stands of coniferous trees and shrubs along the side-slopes of drainages. Riparian forest, dominated by deciduous trees and shrubs, is restricted to Missouri River bottomlands (Fig. 3B). Low shrub and grass dominated vegetation covers most of the remaining area, including ridgetops, coulee bottoms, benches, and some steep south-facing slopes.
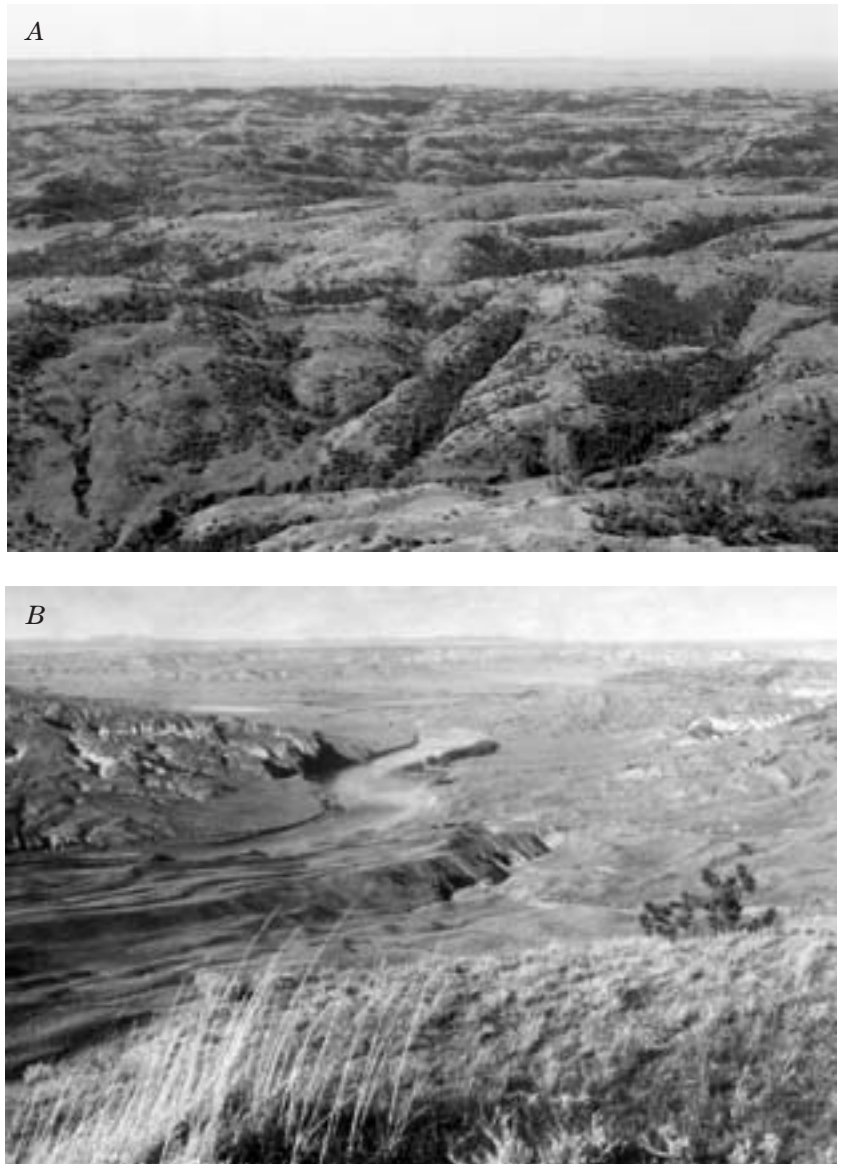
Figure 3.
Timbered breaks environment, Missouri River Breaks study area: upland breaks (A) and bottomland and adjacent slopes along the Missouri River (B).

The climate is semiarid, characterized by moderately low and variable precipitation, low to moderate snowfall, low relative humidity, moderate to strong winds, and great extremes in temperature. Variation in all weather factors is the rule; it influences wide fluctuations in both growing season and winter conditions.

As a result of these environmental factors, the breaks are primarily rangeland. Approximately 75 percent of the area is in public ownership: 45 percent lies within the Charles M. Russell National Wildlife Refuge, 25 percent is administered by the Bureau of Land Management, 5 percent is state land, and 25 percent is privately owned. The human population is low and use of the area is largely related to livestock grazing and recreation.

Timbered breaks have long been recognized as important habitat for mule deer. Although deer populations in the vicinity of our study area declined to extreme scarcity during and following the homestead era, they recovered during the late 1930s and 1940s. The increasing populations focused attention on mule deer by the mid 1940s, and aerial and other surveys provided data on population characteristics and trends from 1947 to 1952. Concern for possible competition among mule deer, elk, and cattle led to an intensive study of interspecific relationships during 1960-64 (Mackie 1970). These studies initiated aerial surveys to determine early winter deer and elk population characteristics and trends through 1974-75.

Prairie-Badlands and Prairie-Agricultural

Studies in the prairie badlands and prairie-agricultural environments were conducted on a 543 km^2 area centered at 47° north latitude, 106° west longitude, approximately 20 km northwest of Terry, in eastern Montana (Fig. 1). Described in detail by Wood *et al.* (1989), the Cherry Creek study area extended about 40 km east to west and 23 km north to south, spanning the drainage divide between the Yellowstone and Missouri Rivers.

The most prominent topographic feature is Big Sheep Mountain which rises 90 m above the divide to an elevation of 1,096 m. The terrain slopes gradually downward from either side of the divide to the lowest elevation (771 m) on the southeast boundary. Drainages are relatively steep and narrow, resulting in a badlands aspect near the divide, but they gradually widen and flatten along their length and develop distinct floodplains toward the perimeter of the area.

The area is characterized by large tracts of open grassland that dominate flat or rolling terrain over 65 percent of the study area (Fig. 4A). Sparsely vegetated badlands and bunchgrass covered hills occur over about 25 percent, mostly in drainage heads. Sagebrush coverage in badlands and grasslands is generally sparse and individual shrubs are typically less than 50 cm tall. Deciduous trees and tall shrubs occur in linear stands along draws through grassland and other habitats. Patches of snowberry and rose occur as long narrow bands in draws above and below the hardwood stands. These shrub and deciduous woodland communities collectively cover only

Figure 4.
Prairie-badlands (A) and prairie-agricultural (B) environments on the Cherry Creek study area.

about 7 percent of the area. Agricultural croplands (Fig. 4B), consisting of dryland grain and legume hay fields, are small (<260 ha) and scattered over less than 4 percent of the area. Livestock grazing and crop production dominate human use on the sparsely populated area that includes about 55 percent federal (BLM) lands, 6 percent state lands, and 39 percent private land.

The climate of the area, like that of the Missouri River Breaks, is semiarid and continental, marked by extreme fluctuations in seasonal and annual temperature and precipitation. Snowfall also is variable, but normally moderate with significant accumulations occurring only rarely.

Historically, mule deer were common in portions of the northern Great Plains that included the study area, while white-tailed deer were locally abundant along some major river drainages and tributaries. Populations of both species declined with increasing human presence in eastern Montana from about 1870 through the early 1920s, but expanded again during the 1940s and 1950s. By 1950, mule deer were sufficiently abundant to damage agricultural crops in the region, while whitetails first appeared on the study area around 1954 (Wood *et al.* 1989). Because the area was typical of the plains environment occupied by both species and was considered important for deer management in eastern Montana, it was selected for comparative ecological studies of both mule deer and white-tailed deer in prairie environments beginning in 1975.

Plains Riverbottom

The lower Yellowstone River extends 350 km from the mouth of the Bighorn River east of Billings to the confluence of the Yellowstone and Missouri Rivers in western North Dakota. Our study spanned approximately 224 km^2 of floodplain and islands between Glendive and Sidney, centered at approximately 47° 30' north latitude, 104° 30' west longitude, in eastern Montana (Fig. 1).

Physiographic features of the area include rolling uplands, alluvial deposits, and a terraced floodplain to the northwest of the river (Fig. 5); and high benches and/or rugged badlands immediately adjacent to the river on the south side. Within the study area, the floodplain was relatively wide, varying from about 2 km above Intake on the upper one-third of the area to 7 km at the lower boundary near Sidney. Elevations on the river varied from 625 m at Glendive to 577 m at Sidney.

Similar to other major riverine environments in the northern plains, natural floodplain vegetation is dominated by the willow-cottonwood-shrubland-grassland sere. This sere originates with willow and cottonwood seedlings becoming established on newly formed sand or gravel bars deposited by annual flooding during May and June. The stands change progressively over some 100 years or more through willow, young cottonwood, mature cottonwood, decadent cottonwood-shrub, and shrub-dominated communities to relatively permanent grasslands. Where undisturbed by natural catastrophe such

Figure 5. Plains riverbottom environment: Elk Island (A) and Intake (B) study areas.

as ice jams during spring runoff or land use for agriculture, complexes of these communities dominate and provide a very diverse vegetative aspect. Scattered small stands of green ash or other deciduous trees may provide further diversity.

Land ownership was predominantly private except for two parcels owned and managed by the MFWP for wildlife habitat and recreation. On private lands, agriculture supported by irrigation of the floodplain and adjacent terraces downstream from Intake was the dominant land use. Croplands occurred as variable-sized fields interspersed with or adjacent to stands of native floodplain vegetation. Sugar beets, alfalfa, corn, and small grains were the principal irrigated crops. Untilled areas were generally grazed by livestock as were tilled areas during autumn and/or winter. Production of livestock, forage crops, and small grains were principal land uses on non-irrigated portions of the floodplain and above Intake. Most of these areas were grazed during autumn and winter as well as during abnormally dry summers when forage production on uplands was poor.

Adjacent to the floodplain, rolling uplands are dominated by open mixed grasslands, while badlands are characterized by steep, sparsely vegetated slopes with stands of juniper along some side drainages. More mesic draws support linear stands of deciduous trees.

Cultivated lands on upland terraces and benches above the floodplain support dryland cereal crops.

During the past century, riverine environments in the northern plains have come to represent habitats of high complexity, diversity, and stability within a region characterized by relative simplicity and high variability in environmental conditions (Dusek *et al.* 1989). High complexity and diversity are provided by interspersion of small units of many different vegetation types or communities, land uses, and agricultural practices along the floodplain. Because of this, areas such as the lower Yellowstone often support extremely high density populations of white-tailed deer that are important in terms of hunting and agricultural relationships.

As a representative bottomland habitat for which baseline data on deer-habitat relations were required to evaluate agricultural relationships and water resource allocation within the Yellowstone Basin (Swenson 1978), the area was selected for intensive studies of white-tailed deer beginning in 1979-80. Some background data for deer populations and habitats in the area were available from studies conducted to evaluate impacts of off-stream water impoundments on wildlife on a portion of the area near Intake during 1976-77 (Swenson 1978).

Northwest Montane Forest

The Swan Valley extends from the Swan-Clearwater divide north to Swan Lake and is bounded by the high and steep-sided Mission and Swan Mountain Ranges to west and east, respectively. Centered at approximately 47° 35' north latitude, 113° 45' west longitude, the valley is 64 km long and 10-16 km wide (Fig. 1). Elevations range from 900 to 1,300 m on the valley floor and from 2,100 to 3,100 m along the bordering mountain ridges.

The Swan Valley is dominated by a subclimax conifer forest that extends the length and breadth of the area (Fig. 6A). Natural openings are few and associated mainly with marshy areas around lakes and ponds and along portions of the Swan River. Other openings occur as a result of human developments on private land along the valley bottom. Collectively, openings comprised only about 6 percent of the area. Stand regenerating events, including logging, the major commercial land use, have occurred over 28 percent of the area since 1900. Most logging has occurred since 1960 and most wildfire occurred prior to 1920. Logging and other timber management patterns vary with the checkerboard land ownership pattern wherein sections of national forest land alternate with sections of private timber company land and state forest land throughout the valley. Harvest units are mostly small but include some up to 260 ha in size (Flathead National Forest 1994).

The climate of the Swan Valley is characterized by moderate summer and winter temperatures. Much of the annual
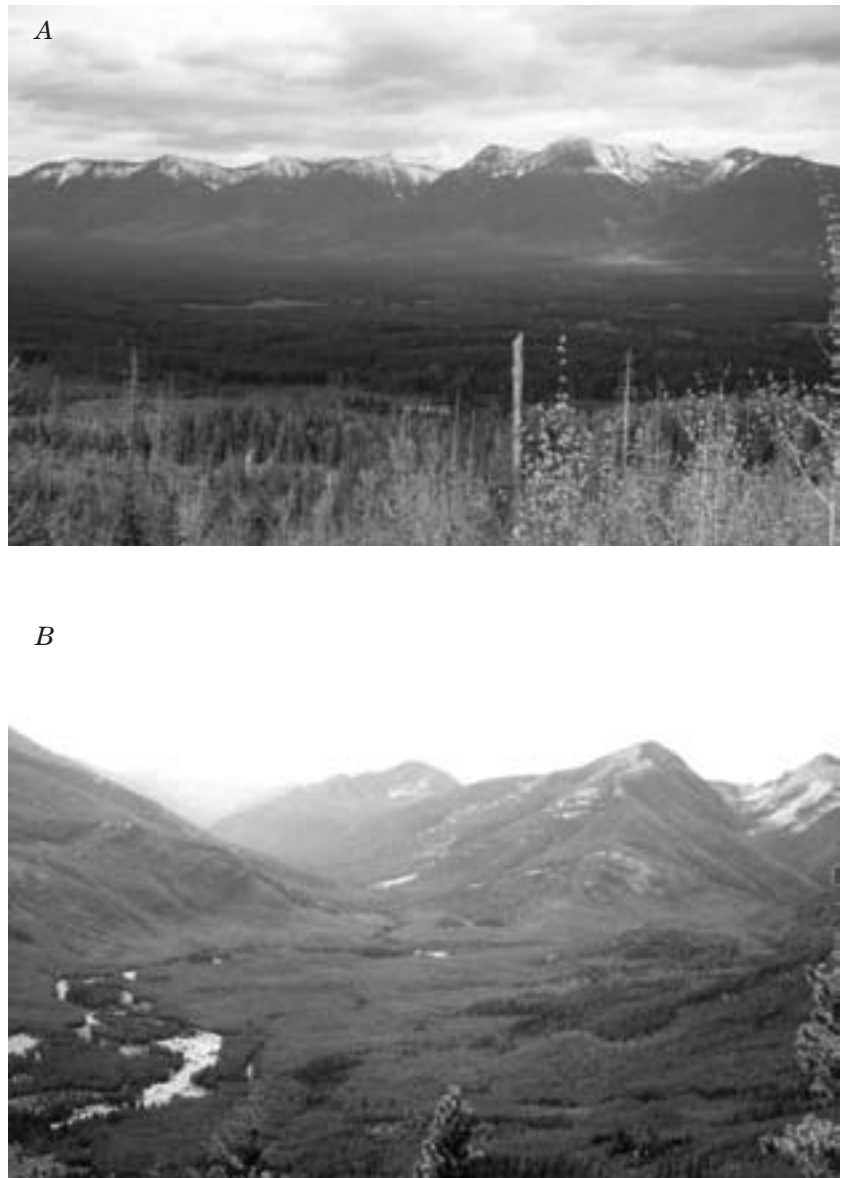
Figure 6.
Northwest montane forest environment: Swan Valley (A) and Salish Mountains (B) study areas.

precipitation occurs as snow in winter such that accumulations are greater and endure longer than in eastern Montana or southwestern valleys.

The Swan Valley is historically important white-tailed deer habitat and representative of the extensive conifer forested mountain valley environment in which the species occurs in northwestern Montana. The area supports large populations of deer that provide significant recreational hunting and are an important consideration in silvicultural practices and other aspects of forest management.

The importance of the deer resource and possible impacts of deer on timber production focused interest on the area in the early 1940s, when the Swan Valley Deer Study became one of the first investigations developed under the Fish and Game Commission's new policy to obtain scientific data as a basis for wildlife management. A graduate thesis study (Hildebrand 1971) on the biology of white-tailed deer on winter ranges in the Swan during 1969 and 1970 also provided background for selection of this area for intensive studies on population ecology of whitetails in 1975 (Mundinger 1981, 1984).

The lower valley, from Condon north to Goat Creek, provides critical winter range for white-tailed deer throughout the valley as well as for deer that migrate seasonally from the Clearwater River drainage. Portions of the valley south of Condon are more highly interspersed with small lakes, ponds, marshes and other mesic/riparian complexes that provide high quality summer habitats but accumulate excessive amounts of snow in late fall and winter. Because of patterns of deer use, our intensive studies focused on winter habitat relationships; summer habitat selection and use was evaluated under a supporting graduate thesis research effort (Leach 1982).

During 1981-82, studies of habitat relationships and population ecology

of white-tailed deer in northwestern Montana expanded to densely forested mountain foothill and valley habitats along the east face of the Salish Mountain Range northwest of Kalispell. Centered at approximately 48° 30' north latitude and 114° 30' west longitude, the primary study area included approximately 480 km^2 in and adjacent to the Tally Lake Ranger District of the Flathead National Forest (Morgan 1993) (Fig 1.).

Topographically, this area is dominated by low to moderate elevation peaks and mountain ridges dissected by several major drainages (Fig. 6B). Slopes are fairly moderate throughout within an elevational range of 915-1,935 m; 60 percent of the area lies between 1,281 and 1,646 m.

Similar to the Swan Valley, the climate is strongly influenced by moisture-laden air from the Pacific northwest that imparts relatively mesic conditions yearlong. Consistent with this moisture regime, over 90 percent of the area is covered by conifer forest with only a few natural grass and shrub openings. Current vegetation is a mixture of mature conifer trees, cut-over areas in various stages of regeneration, riparian areas, and natural willow/grass meadows. Most of the open riparian shrub/grass vegetation is centered in two extensive wet meadow complexes in the central and northern portions of the area. Timber production and recreation are the primary land uses on the area that consists almost entirely of national forest lands. Less than 10 percent is privately owned.

The east slope of the Salish Mountains is an important white-tailed deer habitat complex that, like the Swan Valley, is subject to extensive logging and silvicultural activity. Thus, it offered opportunity for comparative study of habitat relationships of whitetails associated with somewhat more mesic upland habitats on summer as well as winter range.

Habitat Relationships

The Concept of Habitat

Habitat can be defined as ". . .the resources and conditions present in an area that produce occupancy–including survival and reproduction–by a given organism" (Hall *et al.* 1997). Our findings generally support this definition and its application to deer.

In our perspective, deer habitat is not simply a place with food, cover, water, and space; nor is it primarily vegetation or vegetation structure. Rather, we recognize habitat as areas that, based on their physical and biological characteristics, provide for functions contributing to the survival of individuals, populations, and species. These functions include reproduction and maintenance. Reproductive and maintenance habitats may vary considerably in structure, form, and mix of components across species' distributions. They also vary seasonally within areas. They may be interspersed within a single yearlong range, overlap seasonally, or comprise discrete seasonal ranges for deer. However, the fact that they provide for successful reproduction and/or maintenance is the common link for comparison of deer behavior and habitat use among areas.

Reproductive Habitat

On our study areas, reproductive habitat constituted environments with resources required for recovery of physical condition and successful reproduction by deer. Specific attributes varied, but all reproductive habitats provided dependable sources of succulent, high quality forage during fawning and lactation. Thus, they were generally diverse, mesic environments dominated by a variety of forbs or agricultural crops during late spring and summer, though succulent growth of shrubs and grasses also was important. Complex topography that included a diversity of microsites capable of providing alternative sources of some palatable green vegetation through summer also was characteristic. Reproductive habitat provided opportunity for isolation from other deer, security from predation, and minimal competition with other wild ungulates and domestic livestock. High quality reproductive habitat enabled reproducing females to maintain or regain body condition and energy reserves prior to breeding and the onset of winter.

In mountain-foothill environments, reproductive habitat for mule deer occurred most extensively in diverse, mesic montane forests at intermediate elevations (Fig. 7A). High elevation,

...reproductive habitat constituted environments with resources required for recovery of physical condition and successful reproduction by deer.

subalpine-alpine habitats lacked some of the resources necessary to sustain adult females and young. Habitats that consistently provided succulent forage and other resources essential to reproducing females also were limited or patchy in dry foothills and other low elevation habitats.

Reproductive habitat for mule deer was limited and patchy in timbered breaks (Fig. 7B), prairie-badlands (Fig. 7C), and prairie-agricultural environments. There, local areas used by adult females and fawns were topographically and vegetationally diverse habitats that provided succulent forage and visual/spatial isolation from other deer during fawning to late summer. Moderately steep, northerly exposures dominated by diverse, mesic vegetation that sustained some succulent forage through summer were particularly important. In some prairie environments, alfalfa hayfields in or adjacent to relatively steep terrain contributed to the occurrence of reproductive habitat where little or none would otherwise have been available.

Figure 7. Conceptualized distribution of reproductive and maintenance habitat and unused area on the mountain-foothill (A), timbered breaks (B), and prairie-badlands (C) study areas.

Legend:
- ▨ Reproductive
- ☐ Maintenance - winter
- ▦ Maintenance - summer
- ☐ Unused
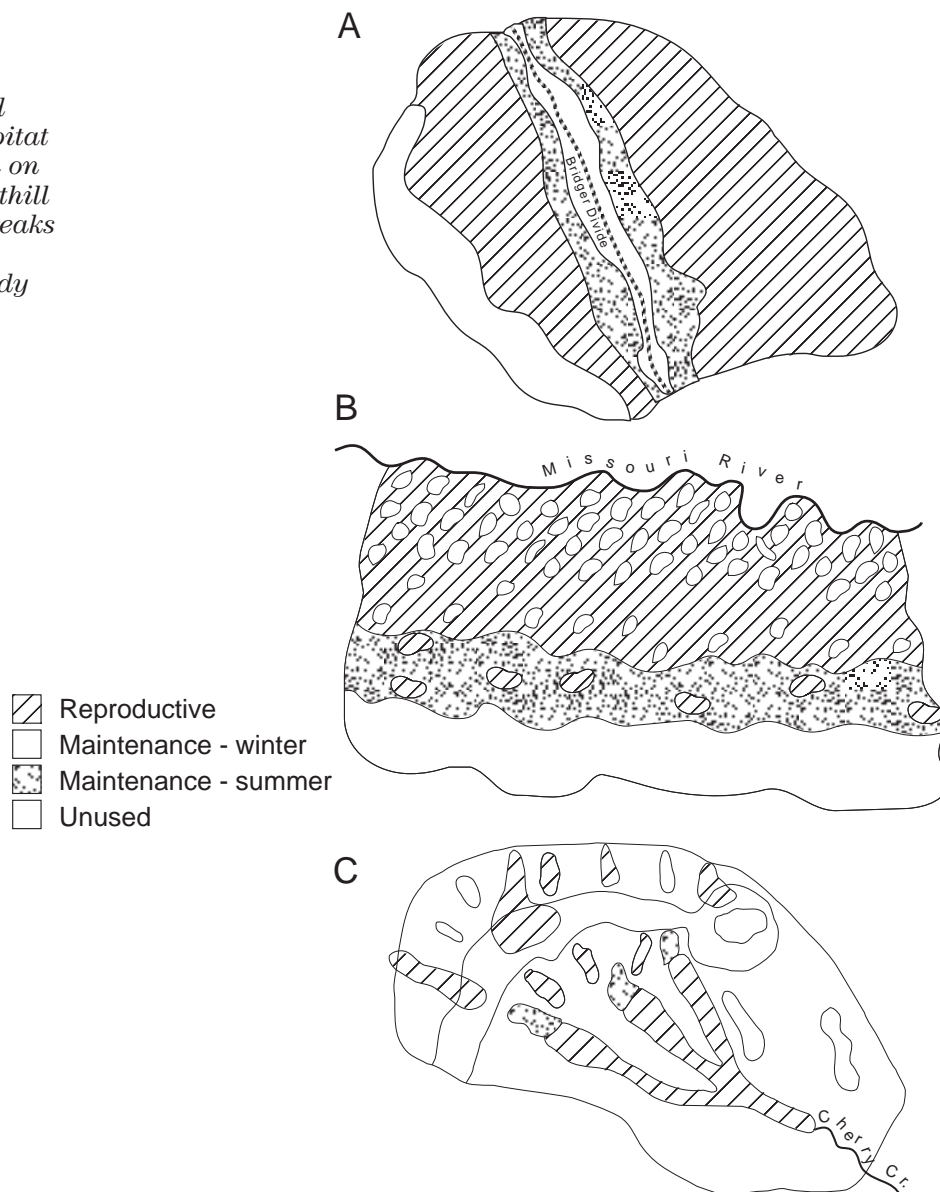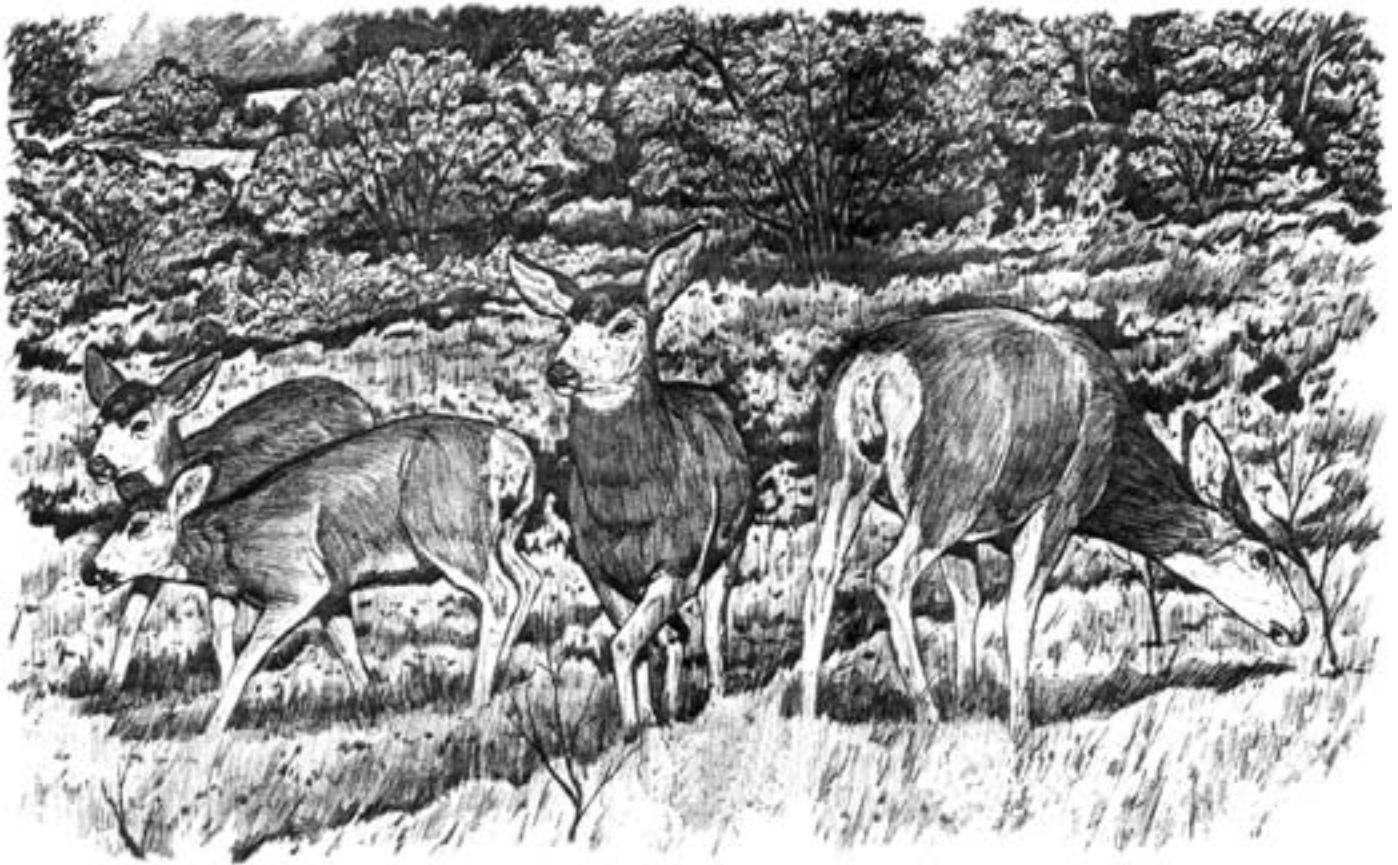
For white-tailed deer, reproductive habitat typically included riparian features such as lakes, ponds, marshes, rivers, or streams. These habitats usually were of low to moderate relief, but vegetationally diverse such that they provided abundant succulent forage from spring to late summer. Agricultural croplands, especially alfalfa fields, in close proximity to riparian cover were an important component of reproductive habitat for whitetails in some plains environments.

Maintenance Habitat

Maintenance habitat consisted of environments that provided all resources necessary for adult survival, but not necessarily recruitment of young. It included summer habitat suitable for sustaining males and nonproductive females and winter habitat for all deer.

Summer

Summer maintenance habitat provided opportunity for males and nonproductive females to grow and recover physical condition. The supply of succulent, high quality forage was inadequate to sustain the additional demands of lactation and reproduction in many years. Summer maintenance habitats tended to be drier, less diverse, and more variable environments than reproductive habitats. Also, risk of predation and/or competition may have been comparatively greater than in reproductive habitat.

Summer maintenance habitats for mule deer in mountain-foothill environments included subalpine-alpine and shrub-grass steppe habitats above and below the montane forest zone, as well as some dry interspersed ridges and slopes. In timbered breaks and prairie-badland environments, they consisted of dry, open habitats of both low and extremely high relief, including gently sloping

Maintenance habitat consisted of environments that provided all resources necessary for adult survival, but not necessarily recruitment of young.

drainagehead and ridgetop areas subject to more intensive livestock grazing.

For white-tailed deer in northwest montane forest environments, summer maintenance habitats characteristically included higher, drier areas with shorter growing seasons than reproductive habitats. In plains riverbottom environments, terrace rangeland interspersed by hardwood draws and mature cottonwood forests, often subjected to continuous livestock grazing, served as maintenance habitat.

Although reproductive and summer maintenance habitat together constituted summer range for deer on our study areas, they are not conceptually equivalent. Summer range traditionally has been perceived as the place deer live from spring through autumn—essentially a homogenous, unlimited summer pasture. Its boundaries are fixed only by the distance deer move from winter range, and may encompass both habitat and areas unused by deer. In most areas, summer habitat is considered unlimited as well as unlimiting to deer populations.

In the context of our findings, however, reproductive and summer maintenance habitat are important functional entities that are spatially and temporally limited. Availability and use of these habitats had direct consequences to population characteristics and dynamics. In variable environments such as the timbered breaks and prairie-badlands, some summer maintenance habitat may become reproductive habitat in wet years and some reproductive habitat may become only maintenance habitat in dry years. In mountain-foothill and northwest montane forest environments the availability of summer reproductive and maintenance habitats is more stable from year to year.

Winter

The broad distribution of winter maintenance habitat for both species of deer in mountain environments was associated with areas receiving minimal snow accumulation. These conditions were created by the interaction of geographic location, topography, climate, and vegetation. Local site characteristics determined the specific location, size, and shape of each winter range and patterns of deer dispersion within it. Vegetation structure and composition were typically only third order factors for mule deer. For white-tailed deer, vegetation augmented other site factors in minimizing snow depth and determining the location, size, and shape of winter habitats.

A dioramic cross section extending west to east through the adjacent Bridger and Crazy Mountain Ranges (Fig. 8), illustrates how interaction among environmental factors influences occurrence of winter maintenance habitats for mule deer. Through geologic processes, the Gallatin Valley floor dropped in elevation while the adjacent surface uplifted and folded to form the Bridger Range. As a result, the west flank of the Bridger Mountains consists of relatively steep west to south facing slopes at elevations between approximately 1,525 m and 1,825 m. Today, these steep, shrub-grass slopes provide a "window of opportunity" for mule deer to survive the winter within a zone of increasing snowfall from the western footslopes to the Bridger Divide. Generally, on this wet, windward slope, snow accumulations below that zone are sufficient to inhibit movement of mule deer to lower valley areas, while snowfall above the zone precludes deer use at higher elevations during all but the mildest winters.

In contrast to the Bridger Range, the Shields Valley attending the west flank of the Crazy Mountains rises gradually from the Shields River eastward to approximately 1,825 m at the point of inflection to relatively moderate mountain slopes above. The lack of steep, open west and south facing slopes combined with increasing snowfall through the 1,525-1,825 m elevational zone precludes opportunity for mule deer to winter along most of the west flank of the Crazy Mountains. Instead, most deer with summer home ranges in montane forest on the west flank migrate around or

Although reproductive and summer maintenance habitat together constituted summer range for deer on our study areas, they are not conceptually equivalent.
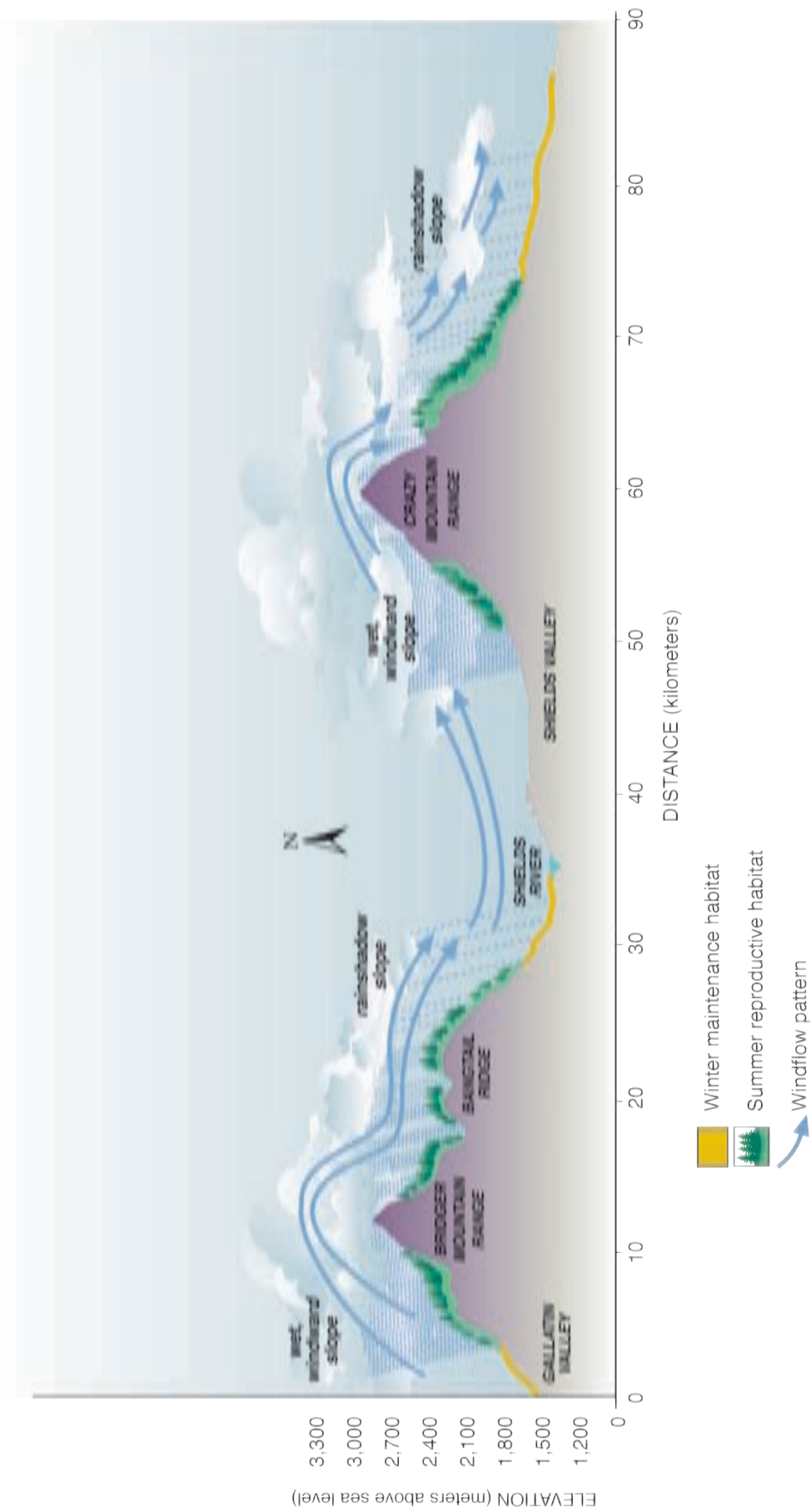
Figure 8.
Diorama showing distribution of important mule deer habitat components as influenced by topography and local climate across two mountain ranges in southwestern Montana.

across the mountains to winter habitat on the north, south, and east flanks (Simmons unpubl.). There, similar to the east slope of the Bridger Mountains, reduced snowfall and other environmental conditions allow mule deer to distribute themselves rather widely over a broad area of rolling, open foothills.

Within this general framework, specific physical and biotic features of winter maintenance habitat varied widely among, as well as across, habitats. Vegetation typically included various mixtures of trees, shrubs, forbs, and grasses, with no particular plant species or combination of species or forage classes appearing to be superior across all, or even adjacent ranges. Individuals, groups, and populations of deer of both species wintered across a spectrum of vegetation varying from essentially open grassland/agricultural cropland to closed canopy coniferous forest and foraged on a wide variety of plant species.

Drought and prior livestock grazing apparently did not reduce deer use of winter range as it did on summer habitat. Winter drought with reduced snowfall typically increased the amount, if not the quality, of available winter maintenance habitat. Most deer winter ranges were grazed by livestock, often heavily. Also, deer of both species occasionally spent part or all winter in or around human-disturbed areas and utilized a variety of food and cover resources to survive.

Studies have shown that most native forages available in winter are too low in nutritional value to meet the maintenance needs of deer (Wallmo *et al.* 1977). Deer survive primarily by supplementing energy reserves accumulated prior to winter with energy intake from submaintenance winter diets. This involves behavior that emphasizes energy conservation. However, deer also selectively foraged under conditions that favor such a strategy, especially in agricultural areas with abundant, high quality forage. On our study areas, stands of coniferous timber and broken topography were important features enhancing energy conservation through

...most native forages available in winter are too low in nutritional value to meet the maintenance needs of deer. Deer survive primarily by supplementing energy reserves accumulated prior to winter with energy intake from submaintenance winter diets.

specialized use of habitat, particularly in deep snow environments. Open environments with limited snowfall or the presence of agricultural croplands fostered selective foraging and more general use of habitat.

These relationships were illustrated by differences in overwinter survival strategies of both species among study areas and habitats. In timbered winter maintenance habitats in the Swan Valley and Salish Mountains of northwestern Montana as well as the Long Pines in the southeast, white-tailed deer behavior emphasized energy conservation. Deer localized on small home ranges in the most favorable thermal environments.

On the lower Yellowstone River, white-tailed deer ranged widely from riparian cover along the river to forage selectively for crop residues in fields throughout the floodplain and adjacent benchlands. They also fed heavily on litterfall that was abundant in stands of riparian cover. In prairie-agricultural ecosystems north of the Yellowstone River, whitetails employed a combination of strategies. Typically, they ranged widely and foraged selectively in dryland grain fields. However, under severe conditions they localized on topographic sites that provided optimal protection from wind chill (Dusek *et al.* 1988).

Winter maintenance habitats along the west flank of the Bridger Mountains could be occupied successfully only when mule deer employed a specialized strategy. This involved utilizing specific microenvironments where snow accumulation was reduced and elevation, exposure, and timber cover provided favorable thermal conditions (Youmans 1979, Pac *et al.* 1991). It also involved restricted movement and generalized foraging where energy expenditure was minimal.

Winter maintenance habitats along the east slope of the Bridgers are very different. With progressively less snowfall at lower elevations, mule deer easily moved below the level of restrictive snow depth to exploit extensive expanses of rolling

shrub-grassland (Pac *et al.* 1991). East slope winter ranges contain few topographic sites offering protection from cold temperatures and the strong chilling winds that characterize eastern foothills. Tree and tall-shrub cover was sparse or lacking. Opportunity for energy conservation in this setting is limited. Instead, mule deer move widely and forage selectively within large home ranges across expansive open ridges. They focus on specific habitats and microenvironments only when conditions are unusually severe.

Unused Areas

Environments lacking resources to sustain deer are largely unused although deer traverse these areas during movement to other habitats. These areas typically lack some component, such as rugged topography or diverse vegetation, and often consist of large blocks of uniform characteristics.

Unused environments for mule deer include large expanses of open rolling grassland, shrub-grassland, or croplands. However, these cover types may comprise occupied habitat where found in smaller units, especially when interspersed with other vegetation or diverse topography.

Unused areas are relatively scarce in mountain-foothill environments occupied by mule deer (Fig. 7A). These areas occur primarily as massive, steep rock formations, alpine scree, and some low elevation basins dominated by monotypic grasslands or dryland grain.

Large, uniform areas of grasslands lacking inclusions of agricultural cropland and/or riparian tree/shrub vegetation were not used by whitetails. Other suboptimal environments for this species were dry shrub-grasslands, breaks, badlands, and montane forest lacking a significant riparian wetland or other mesic component.

The quantity, quality, and juxtaposition of reproductive habitat, maintenance habitat, and unused areas varied (Fig. 7). This in turn affected spatial distribution of deer and the pattern of movement required to use all essential habitat elements.

Areas inhabited by deer were somewhat more heterogeneous in time as well as space than unused areas. Fluctuating environmental conditions influenced plant phenology and the kinds, amounts, and quality of forage and cover available. This influenced fluctuation in the distribution, relative abundance, and quality of the two functional types of habitat.

As noted earlier, the ratio of reproductive to maintenance habitat can fluctuate markedly in highly variable northern plains environments. Livestock grazing, other land uses, and predation were other environmental variables that influenced the amount and effectiveness of reproductive and maintenance habitat available to deer.

The quantity, quality, and juxtaposition of reproductive habitat, maintenance habitat, and unused areas varied. This in turn affected spatial distribution of deer and the pattern of movement required to use all essential habitat elements.

Habitat Selection

Species Adaptations

All members of the deer family are believed to have evolved as species broadly adapted to woodland or forest edge (Putman 1988). Thus, mule and white-tailed deer share many attributes that link them to those habitats. Both species are small bodied, short legged, and similar in head and jaw structure. They have small rumens and a low ratio of rumen-reticular volume to body weight that renders them concentrate selectors in feeding (Hoffman 1985).

At the same time, however, the two species also have evolved individual attributes that constrain each to its own ecological niche and contribute to differences in habitat selection. For example, each species is known by substantial differences in gaits. Mule deer are characterized by a unique four-footed bound or stott (Fig. 9), and white-tailed deer by a long graceful bound with tail flagging in movement (Fig. 10). The structure and musculature associated with the stott by mule deer best fit life and survival in steep, rocky, and relatively open terrain. Conversely, the bounding gait of the whitetail can be recognized as an adaptation to rolling, brushy, or woodland habitats.

Other morphological attributes of white-tailed deer, including the fine-lined body form and ears, brownish coat color, and large, showy tail might also be associated with life in dense deciduous woodland. The heavier build, large mobile ears, excellent distance vision,

Figure 9.
A mule deer in a typical stott.

Figure 10.
A white-tailed deer in a typical bound.

gray coat color with light rump patch, and small, inconspicuous tail of mule deer fit well with life in dry, open, rugged terrain. Among males, the antler form in white-tailed deer may also be associated with life in dense cover; while the large, open, dichotomously-branched antlers of mule deer may be an adaptation to living in more open terrain.

Subtle differences in digestive systems and physiology of the two species also can be associated with habitat selection. Possessing small rumens and gut length relative to body size, deer must eat small volumes of easily digestible food compared with larger ruminants or "bulk feeders" that can eat larger volumes of forage of lower nutritional quality and more difficult to digest (Hoffman 1985). Within this general framework, mule deer, which evolved in drier, more variable environments, seem slightly better adapted to handling larger amounts of coarse forage. White-tailed deer are restricted more to succulent, higher quality foods. The adaptation of whitetails to receive much of their nutrition from plant cell contents and other highly nutritious and easily digestible plant parts (Hoffman 1985, Klein 1985) is particularly evident in the species' close association with agriculture.

Small differences in mouth, jaw, and tooth features between species can also be associated with differences in feeding and habitat selection. Thus, the smaller, more finely structured incisors in whitetails relates to selective feeding and high use of succulent plant parts. Habitat and dietary differences between species also may partially explain differences in patterns and timing of tooth replacement (Dusek 1994).

Other physiological differences influencing habitat selection in deer relate to thermoregulation and adaptations associated with staying warm in winter and cool in summer. These differences appear to stem from long-term adaptation of each species to climates within their primary distributional range.

Although both mule and white-tailed deer are exposed to similar cold winter temperatures, the two species respond differently to decreasing temperatures. Studies by Mautz *et al.* (1985) showed that mule deer were more tolerant of cold, increasing their metabolic rate only when temperatures dropped below -18° to -23° C. Whitetails responded sooner, at temperatures between -12° and -18° C. The difference is assumed related to mule deer being adapted to more open environments with greater extremes in temperature and sharper wind chill than in the wooded cover typically selected by white-tailed deer. The overhead cover requirement of whitetails in winter also may be related to snow and forage conditions locally.

In summer, different mechanisms associated with cooling and water conservation may also encourage habitat segregation. Mule deer that occupy open, dry environments lack sweat glands and rely on panting and possibly dense blood vessels in their large ears to dissipate heat while conserving water. Similar studies have not been made on white-tailed deer, but Parker *et al.* (1985) show that elk, which also select moist habitats with overhead cover in summer, rely on sweating as a primary means of cooling. Although white-tailed deer don't sweat as elk do, their association with moist habitat may be an indication of less heat tolerance.

Behavioral differences associated with habitat selection are exemplified in the manner in which the two species respond to disturbance and their predator avoidance strategies (Lingle 1989, Geist 1994, Wood *et al.* 1994). When threatened, whitetails typically attempt to flee, using speed to put distance between themselves and the disturbance. They follow established trails to ensure swift and sure passage through dense brush. They may also try to hide or take to water to throw predators off their trail. Such behavior would be expected of animals that evolved in rolling, mesic woodland environments.

Mule deer, in contrast, often stand their ground, assess the threat, and may approach, confront, or attack the predator when a threat is perceived.

...the two species also have evolved individual attributes that constrain each to its own ecological niche and contribute to differences in habitat selection.

When threatened, they rely on their four-footed bounding gait to maneuver in any direction, uphill or down, through rough terrain, over and around obstacles to avoid and confuse the predator. The stott, in which the legs are held in, close to the body, also allows the mule deer to kick a predator while fleeing. The bounding gait of the whitetail precludes kicking.

No studies have provided evidence that factors such as social dominance of one species over the other are associated with habitat segregation. In fact, studies have demonstrated that interaction between species typically follows the same individual dominance hierarchy commonly observed within species (Anthony and Smith 1977). Direct interspecific interactions are infrequent and usually nonaggressive. Because of this, we speculate that the species occupying a habitat acceptable to both may depend on which species first became established. This is followed by avoidance of that habitat by the other species as long as the first is able to maintain itself under prevailing environmental conditions.

Process of Habitat Selection

Habitat selection in deer and other ungulates has been regarded as an optimization process. All habitat types and forages in an area are considered available and deer choose those which maximize foraging efficiency and reproductive success. Within this process, other studies have suggested that females select habitat suitable for rearing young, while males select habitat primarily on the basis of foraging opportunities (Geist 1981, Bowyer 1984, Clutton-Brock *et al.* 1987, Jakimchuk *et al.* 1987). This concept is based on differences in energetic requirements and reproductive strategies that exist between sexes in polygynous ungulates (Main and Coblentz 1990).

Our findings agree that forage and other resource requirements are important, but habitat selection also must be interpreted within the constraints of other requirements and traditional behavior of the two species. Habitat selection does not involve random encounter between individual and environment. Most deer, especially females, were limited to selection and use of habitat and resources within or close to their mother's home range. Habitats outside of this area were either occupied by other adult female/family groups or, if vacant, were unknown and potentially available only to a limited number of dispersers. Thus, as concluded by Schoen and Kirchoff (1985), "the composition of the home range was

Most deer, especially females, were limited to selection and use of habitat and resources within or close to their mother's home range.
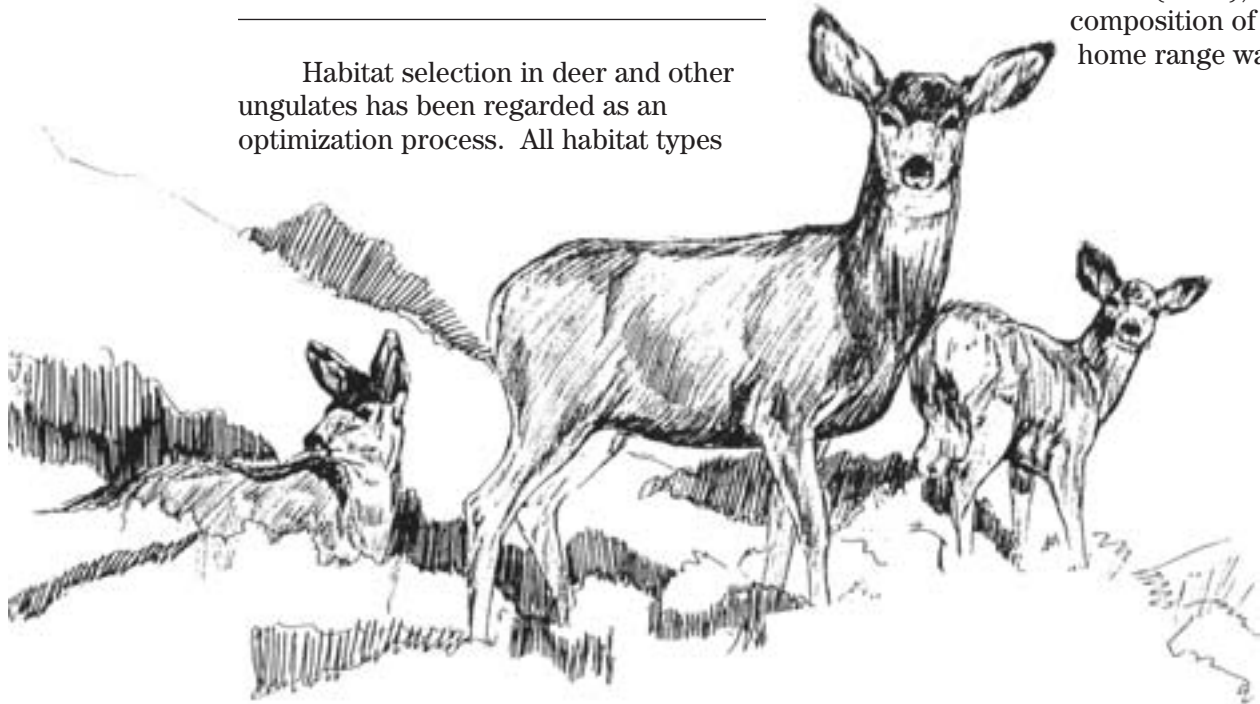
determined by the array of choices available to the individual, and habitat selection was a function of the available choices."

Behavior and Habitat Use

Biologists have long recognized animal behavior as an integral part of life and the process by which species adapt to living with one another and to diversity and variability in the environment (Wilson 1975). Geist (1981) observed that habitat selection, food habits, reproduction, and population dynamics are all accomplished by deer through behavior or closely linked to behavioral adaptation. Our extensive marking and radio-tracking studies confirmed that habitat selection and other deer-habitat interactions are rooted in social behavior and family relationships among individual deer.

Influence of Social Structure

Both mule and white-tailed deer exhibit social structures that are functionally organized around family groups consisting of two or more generations of related females and their offspring. The dominant member or matriarch is a mature female with a history of successful reproduction. At fawning, she occupies a choice area of reproductive habitat that Ozoga *et al.* (1982) called a parturition (fawning) territory within her summer range. This area comprises an optimal mix of terrain and vegetation that provides isolation along with dependable sources of succulent, nutritious forage, hiding cover, and opportunity to escape or evade predators and to avoid competitors. During this critical period of the year, the maternal female isolates herself from all other deer and directs all of her energy to successfully rearing young. Isolation is accomplished through habitat selection and chasing her year-old offspring and all other deer from the fawning territory.

This behavior, by which the mature female maintains exclusive use of that portion of her home range most important to reproductive success, serves as the stimulus for her year-old offspring to begin the process of habitat selection and establishment of their own home ranges. It also serves to allocate important reproductive habitat in an area among several generations of female descendants of the matriarch.

Among yearling females marked in the Missouri River Breaks, 84 percent remained in the area of their natal home range where they established individual home ranges that, at least occasionally, overlapped those of their mothers (Hamlin and Mackie 1989). Typifying this relationship, home range boundaries, observation sites, and fawning territories for one mule deer matriarch in relation to home range boundaries and observations of one of her adult daughters over a 4-year period are shown in Fig. 11. As indicated, total home ranges of the daughter (age 1-5 years) and mother (age 8-12 years) completely overlapped. However, at no time during the fawn-rearing period was the daughter ever observed within the fawning territory of the matriarch.

Figure 11. Home range boundaries and observation sites for a mule deer matriarch and her adult daughter including a June-August fawning territory (after Hamlin and Mackie 1989).

N

| 0 | 0.5 | 1 km |

——————— Mother

- - - - - Daughter

● Relocation sites for mother and/or daughter

Areas used by matriarch during June - August but never used by her daughter during that time after she was one-year-of age.

Fig. 12 conceptually illustrates from observations across all studies how family groups formed clusters of overlapping home ranges in local areas of reproductive habitat. Consequently, resources within the home range of the reproductively successful matriarch, while somewhat diminished for her, were more likely to benefit her descendants than unrelated deer (Clutton-Brock *et al.* 1982, Dusek *et al.* 1989, Hamlin and Mackie 1989, Pac *et al.* 1991, Porter 1991). When fawning territories near the matriarch became filled and unavailable to other deer, yearling or young adult daughters and granddaughters were either displaced to nearby summer maintenance habitats or they dispersed permanently to establish home ranges and new matriarchal groups elsewhere.
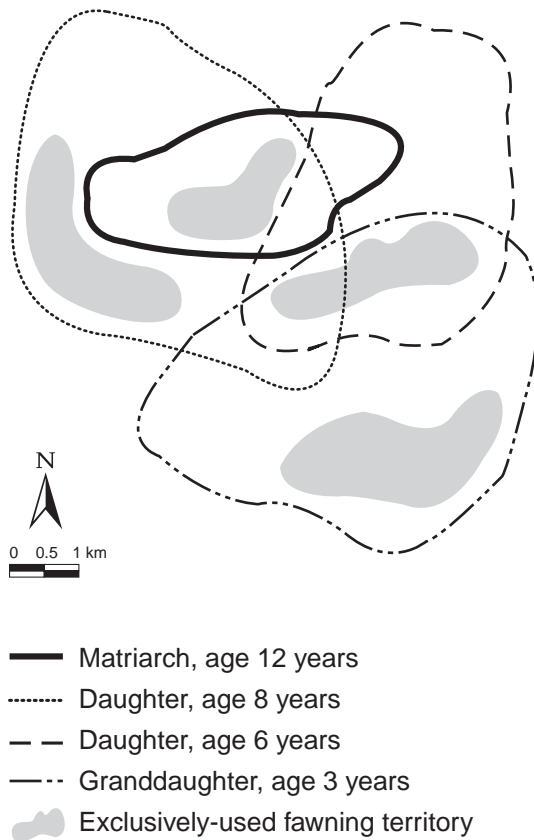
Although matriarchs and adult daughters are often located close to one another, their association in the same social group is influenced by reproductive success. When both matriarch and daughter successfully rear fawns through weaning in late summer, a socially cohesive family group may not reform until late autumn or early winter if at all. Association occurred earlier in summer when related females were barren or lost their fawns.

Fidelity to home range and the long-lasting social bond between mother and most female offspring played a significant role, not only in forming, but also in perpetuating successful habitat use patterns. For example, Fig. 13 illustrates the fidelity of four radio-collared adult female mule deer to individual branches of a drainage system on the Cherry Creek study area. Fig. 14 shows seasonal movement and home range fidelity of a mule deer matriarch, her daughter, and two granddaughters monitored over a 13-year period in the Bridger Mountains.

All four members of the family group in Fig. 14

Figure 12. Conceptualized home ranges and fawning territories of a matriarch and her two adult daughters and a granddaughter during the fawn-rearing period.

—— Matriarch, age 12 years

········· Daughter, age 8 years

— — Daughter, age 6 years

—··— Granddaughter, age 3 years

Exclusively-used fawning territory

0 0.5 1 km

N

Figure 13. Fidelity of four female mule deer to individual branches of a drainage system in a prairie-badland environment. Solid dots represent locations of 2 deer that resided in the lower fork and open circles the locations of two deer that resided in the upper fork of the drainage over a 27-month period (Wood el al. *1989).*

N

0   1   2 km
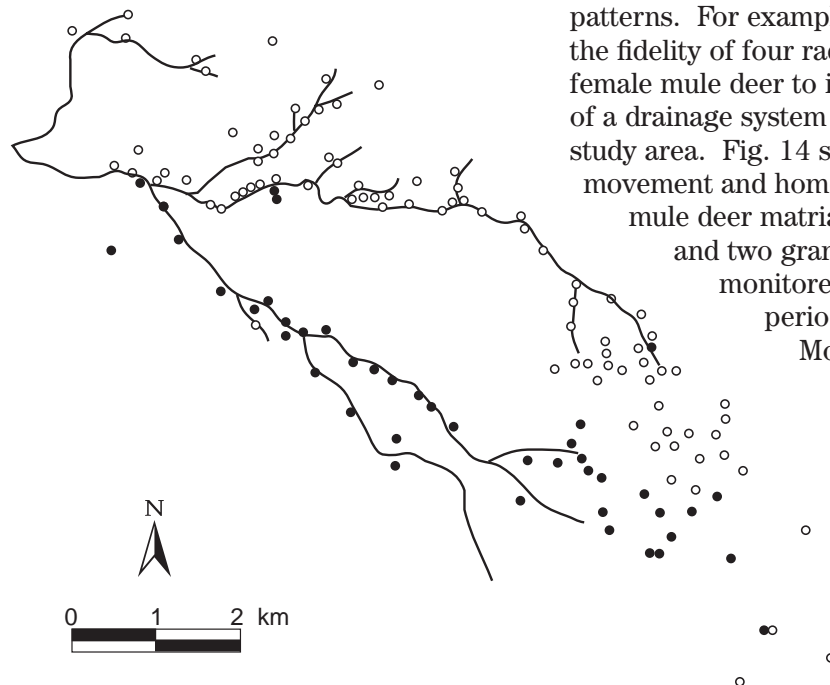
used overlapping winter home ranges connected by a commonly used movement corridor to overlapping summer home ranges east of the precipitous Bridger Divide. Timing of movement across the Divide in relation to snow depth was critical to maintenance of this movement pattern and had to be learned or passed on from matriarch to offspring.

The social system centered on the matriarch, her aggressive behavior, and use of a fawning territory during late spring and summer also influenced spatial distribution and habitat selection by yearling and mature males. Prior to fawning, yearling bucks left or were driven from the mother's fawning territories. Yearling mule deer males appeared inherently more prone to leave their mother's home ranges than yearling females and often dispersed before being chased by their mothers (Hamlin and Mackie 1989). Like mature bucks, yearlings were relegated to maintenance habitats not occupied by productive females.

At 11-14 months of age, 40 (70 percent) of 57 yearling male mule deer marked in the Missouri River Breaks left their natal home ranges; 29 of those (51 percent of all yearling males) left the study area (Hamlin and Mackie 1989). Among yearling male white-tailed deer marked on the lower Yellowstone River, 24 (46 percent) of 50 moved permanently from the vicinity of the mother's home range (Dusek *et al.* 1989). Although a small percentage of yearling males of both species remained on or near their mother's home range, they were seldom included in their own mother's social group. However, yearling males commonly joined, and at least temporarily associated with groups of unrelated does and fawns during late summer, autumn, and winter.

High mobility and variability in movements of yearling males of both species during June-November indicated that most did not establish traditional summer home ranges immediately after breakup of family groups in

spring. Instead, yearling males were social drifters that usually associated with nonproductive adult females or mature bucks (Hamlin and Mackie 1989,
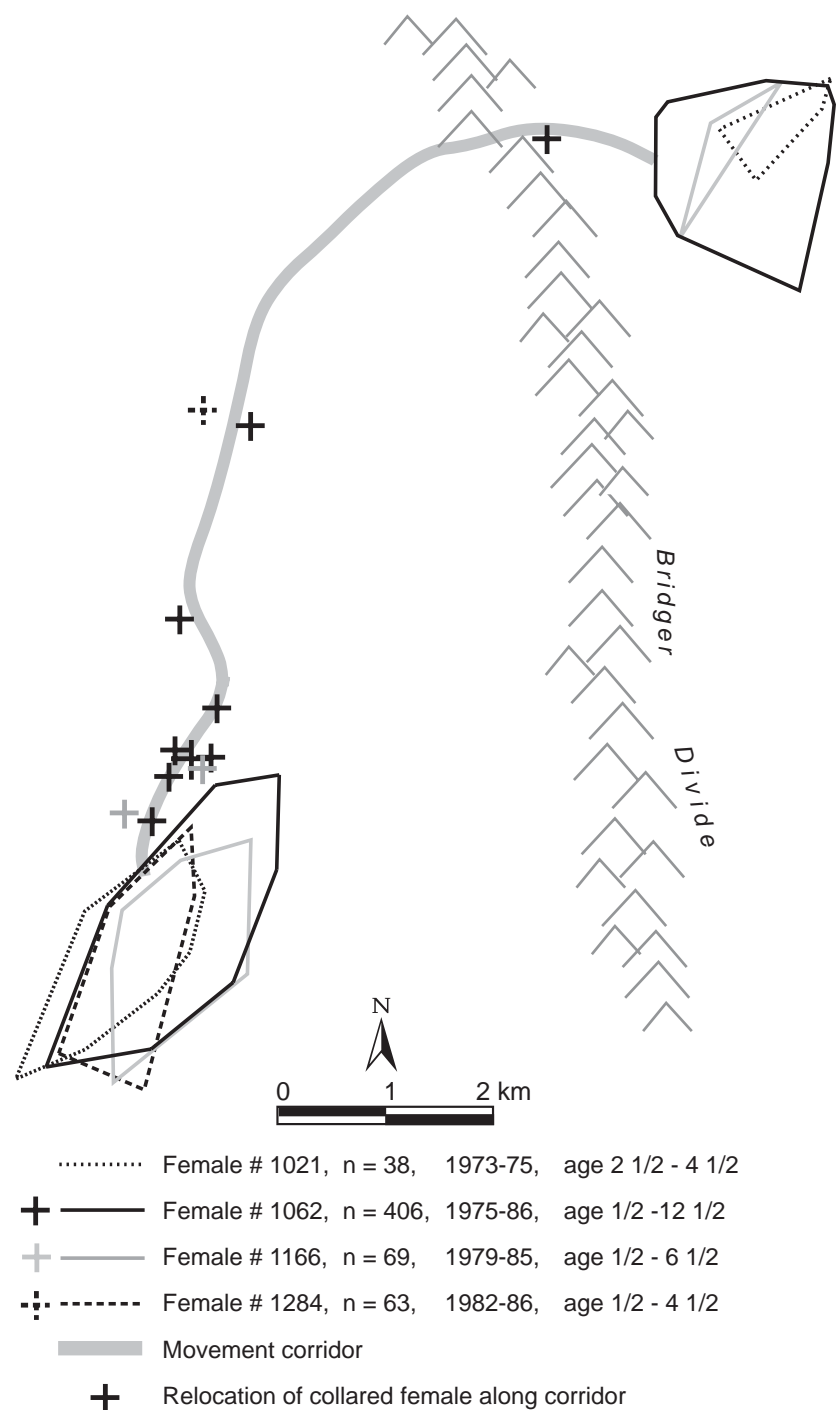
Figure 14. *Seasonal home ranges and interseasonal movement of three generations of related female mule deer in a mountain-foothill environment. Individual relocations during migration indicate a shared movement corridor (after Pac* et al. *1991).*

Pac *et al.* 1991). As a result, most yearling males tended to establish home ranges and other habitat use patterns by mimicking either mature males or tolerant, nonproductive females utilizing maintenance habitats.

Upon reaching maturity, most bucks utilized large home ranges in maintenance habitat where they range apart from productive females throughout the fawning season. During the breeding season, mature males generally expand their movements and home range to have access to as many adult females as possible. As illustrated in Fig. 15, the home range of one mature mule deer buck in the Missouri River Breaks encompassed the home ranges of 11 marked adult females and additional unmarked females.

Interaction of Behavior and Resource Requirements

In late spring and early summer, maternal does of both species on all study areas restricted their movement and sought isolation from other deer on fawning territories. This behavior was related to their needs for succulent, high quality forage to sustain the high energetic and nutrient demands associated with lactation, security from predation for newborn fawns, and avoidance of competitors.

By late summer and early autumn, as fawns were weaned, resource requirements of maternal does changed. Freedom from demands of lactation was followed by need to recover physical condition and develop fat reserves while quality forage remained relatively abundant. The shift in physiological need coincided with a pronounced shift in plant phenology. As native plants mature and produce fruit, nutritional content and values also change, from high protein in succulent, rapidly growing plant materials to high carbohydrate in fruits, seeds, and other plant parts. Thus, does selected habitats that allowed them to maximize energy gathering and intake. They often made specialized use of local habitats and resources that satisfied resource deficiencies experienced on normal seasonal ranges. Movements to agricultural fields with alfalfa, waste grain and row crops, orchards, and other areas represented subtle, yet critically important adjustments in habitat selection that allowed individuals to continue optimal use of habitat in spite of some seasonal deficiencies or changes in local environments.

Late autumn brought severe weather and resource scarcity for deer in mountain foothill environments. Adult does attempted to utilize summer-autumn habitats as long as possible. This delayed their move to winter maintenance habitats which were often characterized by large concentrations of deer on small areas with low quality forage.

In winter, two different patterns of behavior relative to habitat selection and resource use were observed. Deer occupying maintenance habitats dominated by natural vegetation reduced their movement and foraging activity, a strategy to conserve energy and fat reserves. Where deer had access to abundant nutritious forage, especially agricultural crops, movements between bedding and feeding areas suggested a strategy of selective foraging. Spatial separation of females with fawns also

Figure 15. Distribution of home range boundaries for a mature male and eleven adult females (after Hamlin and Mackie 1989).

N

0 1 2 km

—— Home range boundary - mature male
—— Home range boundaries - adult females
• Some locations of the male during the rut
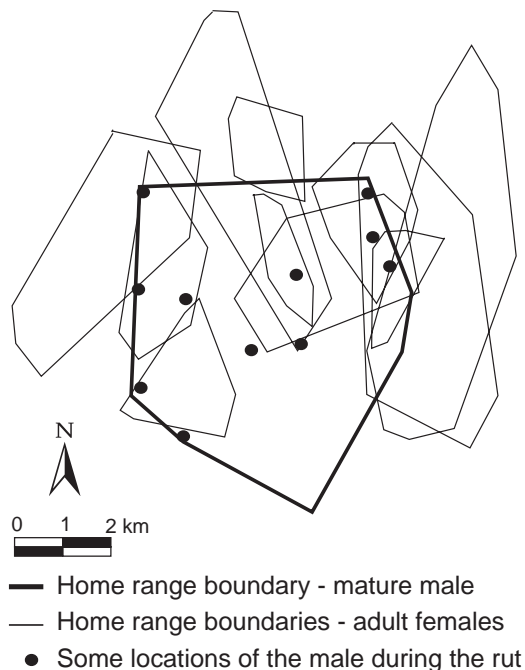
was relaxed as family groups reformed and used the abundant resources. This pattern was most prevalent among white-tailed deer occupying plains riverbottom environments (Dusek *et al.* 1989) but could be followed by deer of either species in any area where agriculture occurred in proximity to natural winter maintenance habitat (Kraft 1989).

In spring, new growth of forbs and grasses strongly influenced habitat selection. Social barriers appeared even more relaxed as deer congregated to forage intensively on local areas with abundant early growth of green plant materials. These usually were located on or near winter maintenance habitats. As soon as snow melt and plant phenology permitted, most adult females moved off winter-early spring ranges to resume use of individual summer home ranges located in timbered habitats offering both security and high quality forage.

The peak energetic demand for reproduction occurs during the rut for males and during late gestation and lactation for females. Therefore, habitat selection unfolded differently between sexes.

During spring and summer, habitat selection of young adult males up to about 4 years of age probably is motivated primarily by their need for resources to sustain body growth and secondarily for antler development. By the fourth year, as individuals achieve mature body size, the requirement shifts more to recovery of body condition depleted during the previous breeding and winter seasons as well as to development of larger antlers. Among mature bucks, antler growth to achieve and maintain social dominance apparently is of equal or greater importance than body growth. However, in heavily hunted populations with few mature males, younger males may face the same increased requirement to recover from the rut in addition to achieving mature body and antler size.

In accord with their different resource requirements, adult males typically were segregated from productive females during summer. The maintenance habitats selected offered access to plentiful forage and selective feeding over relatively large home ranges compared to the small home ranges of adult females. However, they often afforded only limited security from predators. During summer, bucks often associated in loosely organized bachelor groups. Mobility of the groups varied, but often was limited, especially in early summer when habitat selection and use centered on forage-rich sites within the large home ranges.

By early November, rutting dominated the behavior of mature males, and habitat use reflected their search for breeding females. In mule deer, dominant males become particularly mobile and are likely to accomplish most of the breeding. Nonetheless, all bucks exhibit increased mobility as they actively seek to breed as many receptive females as possible. In sharp contrast, dominant whitetail bucks are usually associated with a definitive rutting territory established in dense cover within the overall home range of each individual. Each buck advertises his presence by scent-marking and sign-posting the landscape, and breeds only receptive females that occupy or enter the territory during the rut. If the dominant buck is removed from the rutting territory, he usually is quickly replaced by another buck.

Following the rut, bucks of both species reduce their mobility, shed their antlers, and often move to winter maintenance habitats. Dominant breeding males tend to be in poor condition following the energy-costly rut. Because of this, and faced with a prolonged winter energy deficit, habitat selection and use reflect conservation of remaining fat reserves. Some segregation of the sexes usually occurs unless severe winter conditions force concentration and aggregation of all deer on limited habitat.

By spring, adult bucks selected habitats that provided greatest opportunity to recover physical condition. Foraging activity focused on new plant growth that was available in large quantities at low elevations. In contrast to females with fawns, the lower security requirements of bucks allowed them to make prolonged use of these open,

The peak energetic demand for reproduction occurs during the rut for males and during late gestation and lactation for females Therefore, habitat selection unfolded differently between sexes.

forage-rich areas. Because of this, bucks often returned to summer home ranges somewhat later than adult females.

Patterns in Habitat Selection
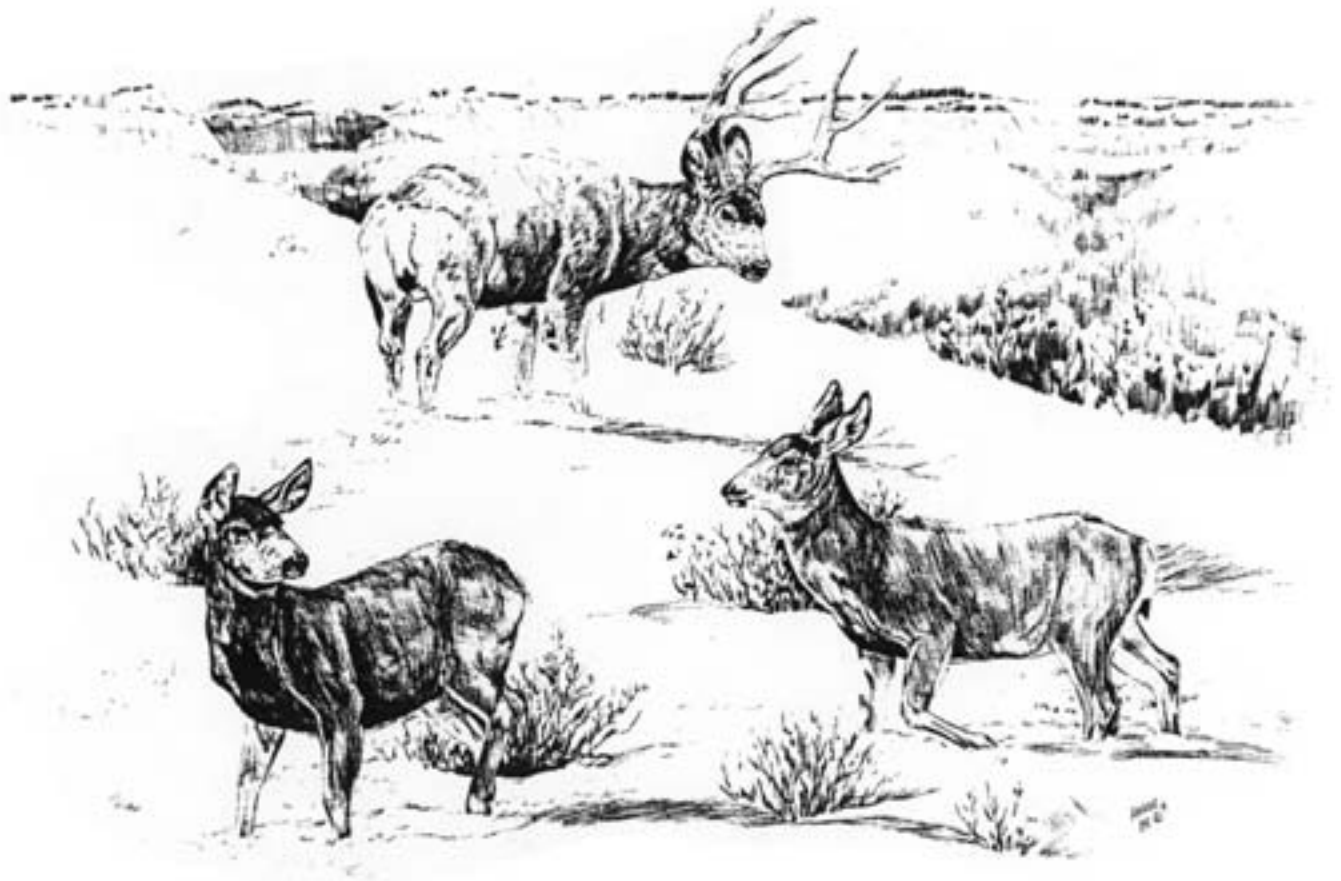
We found that as environment varied, patterns of distribution and movement, use of vegetation/cover types and forage, activity regimes, and sociality also varied. Habitat selection in both species unfolded as a three-step process associated with establishment of individual home ranges. The first occurred at the landscape level and involved the broad behavioral strategy and habitat use necessary to settle into and successfully exploit a particular environmental complex. It usually involved individuals adopting seasonal habitat use patterns that mimicked proven strategies of their mothers or a social

group to which they became attached. At the second or individual home range level, each deer "fine-tuned" its own habitat selection and use to the structure and resources of the local area it attempted to exploit. At the third level, individuals continually adjusted their habitat use patterns or behavior within individual home ranges to fluctuations and ongoing changes in local environmental conditions. Over time, effective exploitation of the diverse environments we studied involved numerous adaptations and adjustments in behavior.

Distribution, Movements, and Home Range

Spatial distribution, movement, and home range patterns of individual deer of both species centered in three general strategies that formed a continuum of increasing specialization: residency; adjacent seasonal home ranges; and distinct seasonal home ranges.

The first and most fundamental strategy that a deer can use in exploiting its local environment is yearlong residency or use of indistinct seasonal ranges. Deer used single yearlong home ranges where the basic requirements of maintenance and reproduction could be satisfied within one local area and microsites important for seasonal requirements were dispersed throughout the area. As a result, a deer could generally occur in any portion of the resident home range at any time of the year (Fig. 16). However, certain portions often received more use during some seasons.

When resource requirements could not be met in one local area, specialized movements and use of home range began to develop. Deer with adjacent seasonal home ranges used identifiable winter and summer home ranges that were usually separated by only a few kilometers (Fig. 17). Adjacent seasonal home ranges represent a blend of both residency and migration. Although a greater proportion of locations typically occurred in one area during a season, deer following this pattern tended to move back and forth between the two seasonal home ranges.

Deer used distinct seasonal home ranges when a relatively high degree of specialization was required to exploit a particular environment (Fig. 18). Winter and summer home ranges were distinct entities separated by distances of a few to as much as 130 km. As the distance between seasonal home ranges increased, movements more closely resembled true migration as described by Baker (1978). Intra-seasonal trips between the seasonal home ranges were the exception and almost never occurred among mule deer with winter and summer home ranges centered more than 5 km apart in mountain-foothill environments (Pac *et al.* 1991).

The general type of movement patterns employed by deer depended on the spatial arrangement of important habitat components that they attempted to exploit. Among our study areas,
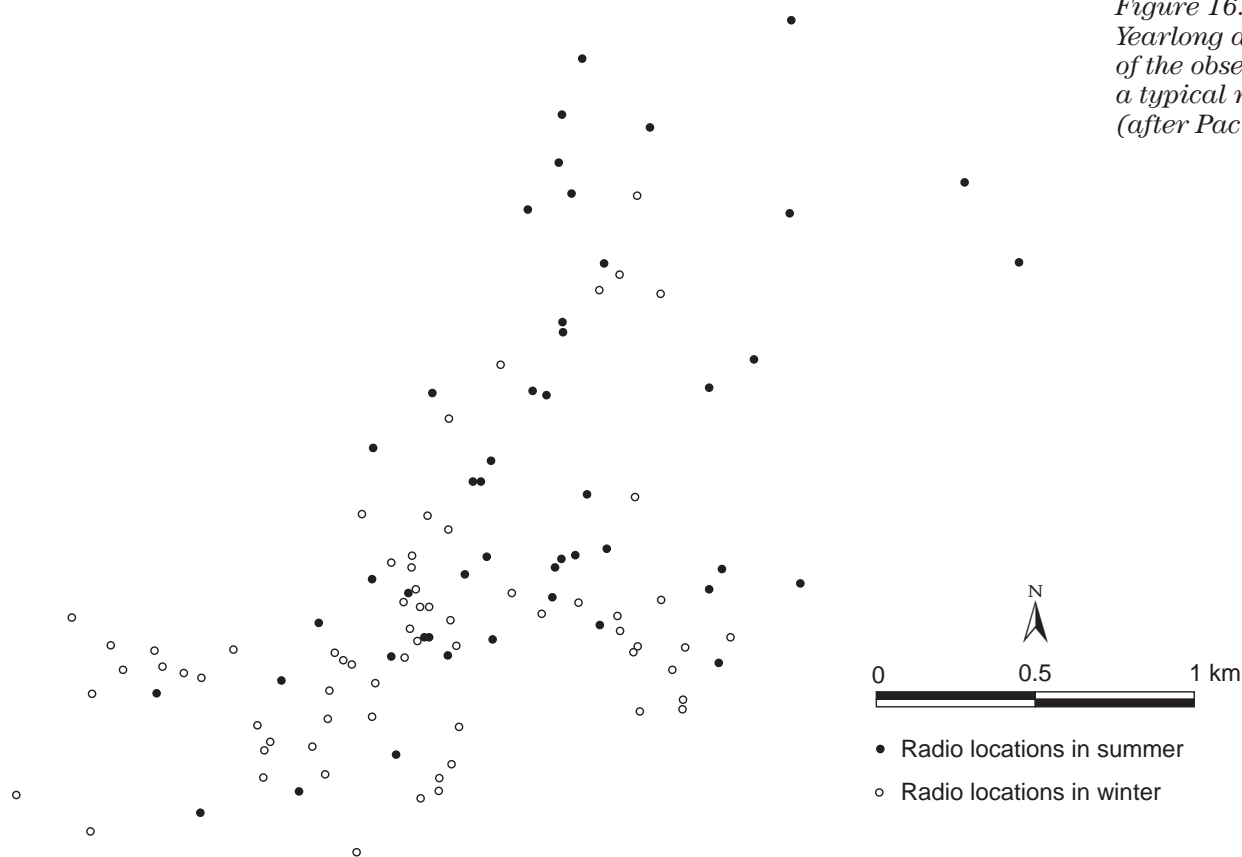
Figure 16. Yearlong distribution of the observations of a typical resident deer (after Pac et al. *1991).*

0   0.5   1 km

● Radio locations in summer

○ Radio locations in winter
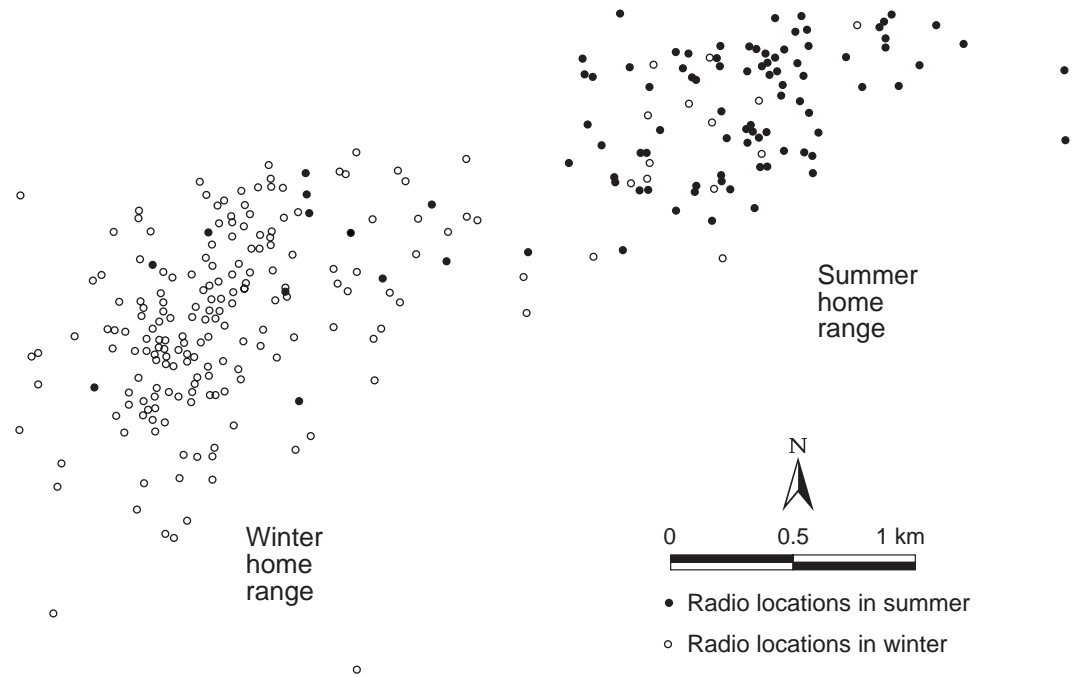
Figure 17.
Yearlong distribution of the observations of a typical deer with adjacent seasonal home ranges (after Pac et al. *1991).*
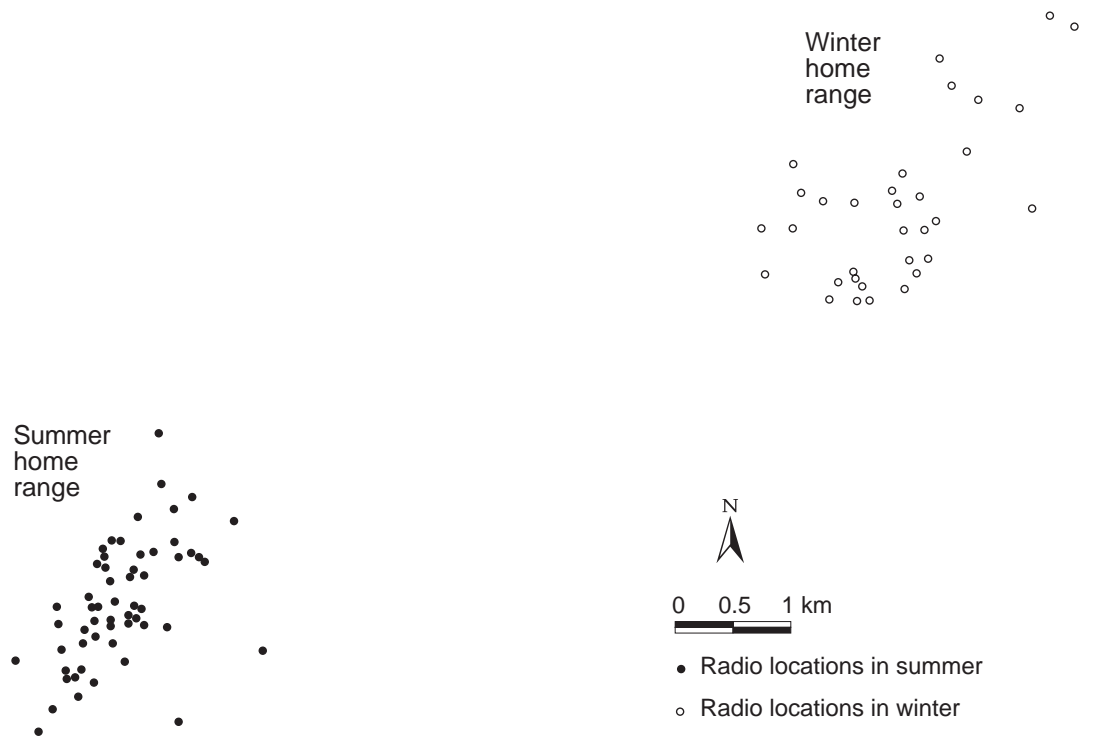
Figure 18.
Yearlong distribution of the observations of a typical deer with distinct seasonal home ranges (after Pac et al. *1991).*

classification of entire populations of deer according to one of the three movement patterns was rarely appropriate. Rather, each environmental setting occupied by deer usually produced a mosaic of individual strategies that included all three patterns.

The residency pattern was common in environments where winter maintenance and reproductive habitats overlapped or were closely interspersed. For example, the resident pattern described approximately 90 percent of mule deer occupying reclaimed habitats near the Colstrip mine in southeast Montana (Fritzen 1995) and 100 percent of mule deer on the Dog Creek study area in sagebrush grassland habitat of northeast Montana (Jackson 1990). About 80 percent of the white-tailed deer inhabiting irrigated floodplains of eastern Montana (Dusek *et al.* 1989) displayed this pattern as did 30-40 percent of mule deer inhabiting prairie-badlands (Wood *et al.* 1989) and 60 percent of those in the Missouri River Breaks (Hamlin and Mackie 1989).

The residency pattern accounted for only 10-15 percent of mule deer inhabiting mountain-foothills of southwest Montana (Pac *et al.* 1991) and east front ranges in northcentral Montana (Kasworm 1981, Ihsle 1982). Similar proportions of resident white-tailed deer were documented in the northwest coniferous forests (Morgan 1993). However, the proportion of resident deer increased to approximately 30% in mule deer populations occupying a northwest montane forest environment (Stansberry 1996).

Use of adjacent and distinct seasonal home ranges was most prevalent among deer of both species inhabiting strongly seasonal mountain environments in central and western Montana. In these settings, winter maintenance habitats often were distributed in a narrow belt or in specific patches at lower elevations. Winter ranges typically provided yearlong habitat for small numbers of deer. Most reproductive and summer maintenance habitat was located in relatively large expanses of montane forest at middle

to higher elevations. Thus, most deer exhibited seasonal movement between adjacent or distinct seasonal home ranges. Deer utilizing these two patterns made up 70 percent of the mule deer inhabiting the west slope (Stansberry 1996) and 90 percent of all whitetails along the east slope of the Salish Mountains (Morgan 1993). These patterns also were employed by 85-90 percent of all mule deer in mountainous environments of southwest and northcentral Montana (Pac *et al.* 1991, Kasworm 1981, Ihsle 1982).

Even in the more gentle topographic settings of eastern Montana, use of spatially separated seasonal home ranges was common among deer in upland areas where reproductive and winter maintenance habitats were patchy and separated. These patterns typically involved movement of deer from reproductive and summer maintenance habitats in areas of low topographic relief to winter maintenance areas in steeper terrain and lower snow accumulation.

About 40 percent of the deer studied in the Missouri River Breaks displayed movements similar to either the adjacent seasonal home range or distinct seasonal home range patterns (Hamlin and Mackie 1989). On the Cherry Creek study area, about 45 percent of the mule deer followed these patterns; 25 percent were described as "autumn migrants" (Wood *et al.* 1989). Each autumn migrant utilized one home range most of the year, but occupied a distinct autumn range from mid-August to mid-October.

On the upland prairie-agricultural habitats associated with the Cherry Creek study area, Wood *et al.* (1989) concluded that female white-tailed deer exhibited individual movement patterns that were difficult to categorize. Some used small, stable home ranges while others made erratic shifts among several seasonal activity centers within large home ranges.

Our studies confirmed that more specialized movement patterns among adult females probably developed from a requirement for an exclusive fawning territory. Among females that shared a local area of winter maintenance habitat, not all found suitable fawning

The general use of movement patterns employed by deer depended on the spatial arrangement of important habitat components that they attempted to exploit.

territories in that vicinity. Aggression by established resident matriarchs forced some female offspring to seek out and establish their own fawning territories at some distance from the established family group. Females that developed these new adjacent seasonal home range or distinct seasonal home range traditions would be expected to pass on successful patterns to subsequent generations.

Fine-tuning the Home Range

Individual deer "fine tuned" their home range to changes in the local environment by incorporating subtle adjustments in their movements and habitat use. Across the environments we studied, this process occasionally involved specialized use of accessory areas usually located outside of normal seasonal home ranges. Deer used these areas to satisfy temporary resource deficiencies experienced within the normal home range.

Knowledge of accessory areas was learned through exploration or by associating with other deer using these areas. Once individuals were monitored for sufficient time to identify these subtle specializations in habitat use, the factor or circumstance influencing the movement was usually evident. Even though accessory areas were not occupied in the traditional manner that seasonal home ranges were used, their use was relatively predictable based on environmental conditions. Use of seasonal accessory areas was responsible for much of the variation observed among individual deer movement patterns.

Although any number of seasonal accessory areas might occur, we identified five different types used during winter, spring, early summer, late summer, and autumn in the Bridger Mountains (Pac *et al.* 1991). Conceptual examples (Fig. 19) show how use of various types of accessory areas allowed deer to adjust their movements and home range to changes in the local environment.

Figure 19. Conceptualized home range patterns and accessory areas showing increasing specialization in the use of space by season. Individual telemetry locations are labeled by season: W=winter; S=summer;. F=fall, Sp=spring. Accessory areas are shaded.
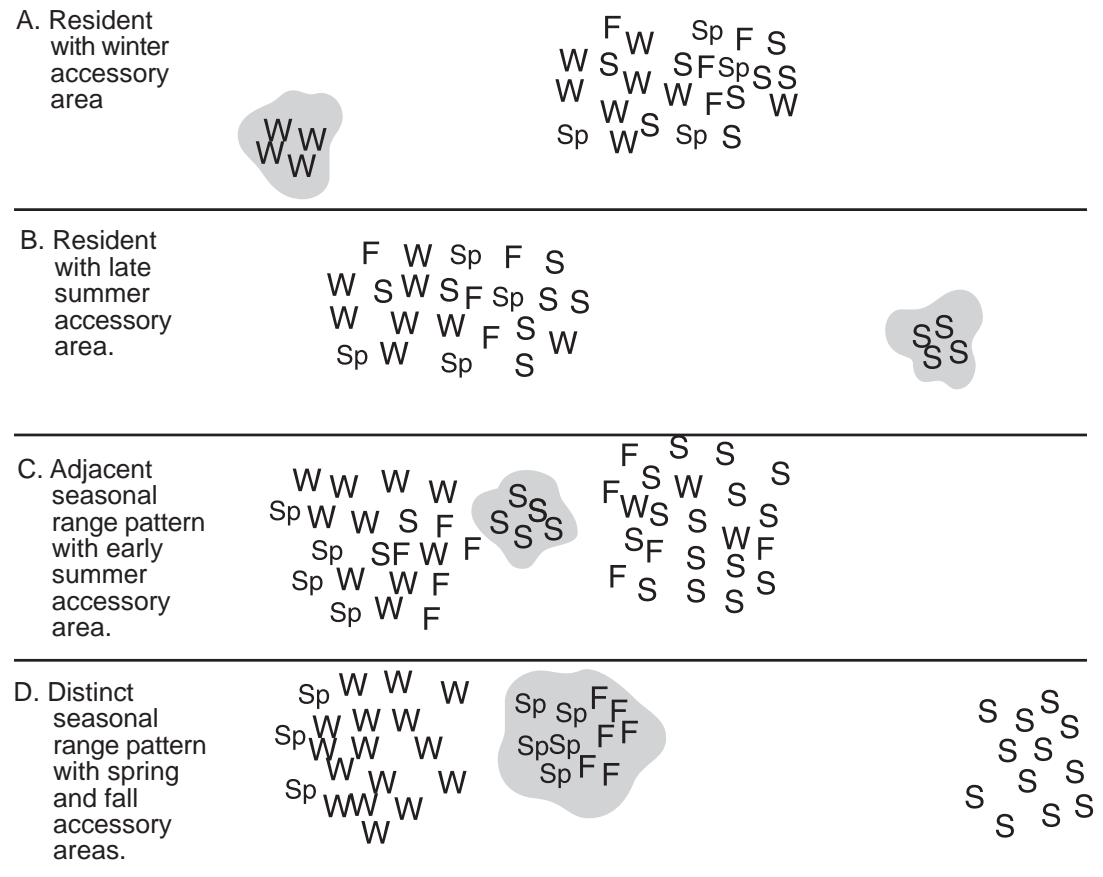
Resource requirements of resident deer are generally satisfied within one home range (Fig. 19A). During occasional severe winters, resources available within the normal home range of some deer became inadequate as a result of deep snow and cold winds. Under such conditions, these individuals temporarily abandoned their normal home range and moved 1-20 km directly to site-specific winter accessory areas that offered more tolerable snow depths and greater topographic relief. These areas provided more plentiful, steep south slopes with warm microsites that were often in close proximity to conifer stands with dense canopies.

Hamlin and Mackie (1989) noted that improved forage availability did not appear to be the incentive for moving to winter accessory areas in the Missouri River Breaks. There, these sites typically offered the poorest quantity and quality of forage among all vegetation types. Use of winter accessory areas favored energy conservation, ease of mobility, and escape from predators.

During severe winters in the Missouri River Breaks and sagebrush grasslands in northeast Montana (Jackson 1990), use of winter accessory areas outside of the normal home range was a common occurrence. Use of accessory areas during severe winters in mountain country was usually limited to resident mule deer occupying home ranges with low topographic complexity, although a few deer with adjacent and distinct seasonal ranges used these areas (Pac *et al.* 1991). Time spent on these areas was usually confined to the duration of severe conditions. Individual deer rarely used winter accessory areas in consecutive years unless severe conditions occurred in successive years. We suspect that white-tailed deer employed similar strategies during severe winters.

Use of late summer accessory areas by resident deer (Fig. 19B) usually coincided with desiccation or killing frosts which reduced the availability of green, succulent forage during late summer. Succulent forage in late summer was particularly important for adult

females attempting to recover from the demands of lactation. Most deer located alternative sources of succulent forage inside the boundaries of their home ranges. However, during very dry years, some deer moved 1-14 km beyond normal home range boundaries to late summer accessory areas located near alfalfa fields, hay stacks, riparian communities, or to areas of greater topographic complexity that offered moist sites and succulent, native forage. In the Missouri River Breaks and the Bridger Mountains, normal home ranges of resident and migrant mule deer using late summer accessory areas were generally located in areas of relatively low topographic complexity and were heavily grazed by domestic livestock (Hamlin and Mackie 1989, Pac *et al.* 1991). Accessory areas were invariably located in habitats ungrazed by livestock at that time. Deer used late summer accessory areas more frequently than winter accessory areas, but not every year.

The autumn migrant pattern displayed by individual mule deer on the Cherry Creek study area (Wood *et al.* 1989) was similar to use of late summer accessory areas by resident deer. However, autumn migrants moved outside of their normal home ranges each year to areas with deciduous shrubs. Habitats used by these deer during most of the summer contained less badlands than those used by resident deer. Autumn migrants commonly experienced shortages of succulent forage in early autumn within their home ranges. This forced them to move to more suitable habitats at lower elevations.

The search for high quality forage in late summer also influenced movements of whitetail does, even in riverbottom environments. Herriges (1986) reported that the proportion of whitetails moving to agricultural fields increased in late summer as fawns were able to travel with their mothers and native forages became desiccated. These movements contrasted with the definition of a late summer accessory area because they represented a strategy that occurred every year, usually within the confines of

the home range. However, the motivation for patterns of habitat use in late summer was essentially the same in both species.

In rugged mountain habitat, adult female mule deer often exploited high elevation summer home ranges in close proximity to their winter home ranges (Fig. 19C). Although the seasonal ranges may be only 1-5 km apart, the change in elevation may exceed 435 m. Use of early summer accessory areas was relatively common among mule deer in these situations and appeared to be related to resource requirements associated with fawn-rearing (Pac *et al.* 1991).

Beginning in late May and early June, as snow melt reached higher elevations, mule deer does following adjacent seasonal home range movement patterns moved directly to their summer home ranges. In some years, however, new plant growth was not sufficiently advanced at higher elevations to support the high demand for succulent forage associated with lactation. Under such conditions, does occupying these habitats were forced at fawning to move down to early summer accessory areas located near their winter home ranges. While the more open sites provided adequate sources of succulent forage, they may have offered limited security for newborn fawns. Choice sites offering both security and succulent forage occurred at intermediate elevations, but these sites were usually occupied by other maternal females that defended them against intruding deer during the early fawn-rearing period.

Pac *et al.* (1991) reported that early summer accessory areas were located an average of 2.3 km from summer home ranges and almost 420 m lower in elevation. Use of early summer accessory areas along the west slope of the Bridger Mountains generally occurred during June 17-July 17. This period corresponded closely to the 30-day period around fawning when maternal does are aggressive toward other deer (Ozoga *et al.* 1982).

Early summer accessory areas apparently represented a specialized strategy that allowed females to exploit high elevation habitats that were limited in resources during early fawn-rearing. Use of such areas by deer in lower elevation environments apparently is rare. Pac *et al.* (1991) reported that one resident mule deer doe used an early summer accessory area on the Brackett Creek winter range. Fritzen (1995) described a similar pattern for a resident mule deer doe on his study area near Colstrip.

Deer that migrate between distinct seasonal home ranges often incorporate the greatest degree of specialization into their annual movement patterns. These individuals not only travel the longest distances, but also exploit environments that require additional adaptations in movement and habitat use. Typically, use of some type of spring and/or autumn accessory area is involved (Fig. 19D).

Pac *et al.* (1991) reported that use of spring and autumn accessory areas was greatest among deer that crossed a major mountain divide or encountered substantial elevational relief along movement corridors connecting their seasonal home ranges. Both types of accessory areas were usually situated closer to the winter home range and at elevations intermediate to winter and summer home ranges. Some individuals only used spring accessory areas, others only autumn, and some used both types. Spring and autumn accessory areas were used with greater regularity than other types of accessory area.

Deer of both species occupying mountain environments attempted to leave winter concentration areas in spring as snow melted and greenup began. In most cases, only resident deer remained on or near winter ranges. Some individuals using adjacent seasonal ranges with summer home ranges located at low-middle elevations moved early and directly to summer range. Others, as well as deer with distinct seasonal ranges in or across high elevation habitats, moved to spring accessory areas concomitant with early growth of herbaceous forage plants at intermediate elevations.

Spring accessory areas tended to be site-specific for individuals or family

groups, though overlap often occurred in areas of high deer density. Because deer preferred to move to summer home ranges as soon as possible, spring accessory areas were generally occupied for shorter periods than autumn areas. Pac *et al.* (1991) reported that individual mule deer used spring accessory areas from 15-40 days compared to 30-65 days for autumn areas. Spring snow storms and cold temperatures resulting in persistent snowpack resulted in later or prolonged use of spring accessory areas in some years.

The extent to which deer tolerated snow on their summer home ranges varied widely among individuals depending on when the snow occurred, the juxtaposition of their summer and winter ranges, and the topographic characteristics along their movement corridors. Deer with summer home ranges on the opposite slope of a high mountain divide from their winter ranges were the first to respond to autumn snowstorms and move to autumn accessory areas. Weather conditions on the divide, rather than on the summer home range, dictated when these deer moved. Pac *et al.* (1991) reported that mule deer exploiting high elevation summer ranges spent about 70 fewer days on summer home ranges than deer exploiting lower elevations in the same mountain range. Deer remained on autumn accessory areas as long as snow depths were tolerable. Deer that did not use autumn accessory areas moved directly to winter ranges, usually later in autumn or early winter following snow that precluded continued use of summer ranges. Severe weather accelerated autumn movements and resulted in earlier concentration on winter ranges.

Mule deer bucks exhibited a different pattern of use of spring and autumn accessory areas than females (Pac *et al.* 1991). In spring, some yearling and mature males remained on winter home ranges and spring accessory areas for up to one month longer than adult females. This appeared to be consistent with a male strategy of habitat use that emphasized forage gathering in open areas at a time when they were gregarious. Bucks did not experience the same requirements for isolation and security that caused adult does to move as soon as possible to their summer home ranges. Bucks were more "casual" in their movements and tarried along their movement corridors as long as they were able to find adequate succulent forage. These differences in timing of movements between the sexes provided adult females with unrestricted choice of summer habitats before males arrived to "fill in the holes" at a later date. Because of this, increased population size resulted in relegation of adult males and younger adult females to summer maintenance habitat.

During autumn, use of accessory areas by mule deer bucks in mountain-foothill environments was less site specific because of greater mobility associated with the breeding season. Rut-related movements often were tangential to the normal, linear orientation of their movement corridors. Some bucks temporarily moved to higher elevations; others crossed intervening ridges and moved into drainages not used during other seasons. During the rut, a few moved as much as 11 km from their normal ranges while others showed no noticeable expansion of their home range.

Home Range Size

Home range size was part of the habitat use strategy employed by individual deer to exploit the environments they occupied. Extreme individual variability in home range size was characteristic of home range measurements in all environments. This indicated that mobility and home range size represent adaptations unique to individuals and the habitat they occupy. Home range parameters expressed as means for populations or habitats must be viewed as generalizations and interpreted with caution.

Home range sizes and relationships in the various environments we studied are described in detail in other reports (Dusek and Mackie 1988, Dusek *et al.*

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1989, Hamlin and Mackie 1989, Wood *et al.* 1989, Pac *et al.* 1991). Generally, however, males had larger home ranges than females. Among resident deer monitored in our studies, annual home ranges of mule deer bucks in the Missouri River Breaks (Hamlin and Mackie 1989) averaged 27 km^2 compared to only 5.2 km^2 for white-tailed bucks along the lower Yellowstone River (Dusek and Mackie 1988). Annual home ranges of resident females in those environments averaged 5.2 km^2 and 1.1 km^2, respectively.

Migratory deer exhibited smaller seasonal home ranges than resident deer which could use all portions of their annual home ranges during all seasons. Average summer home ranges of adult female mule deer with distinct seasonal ranges in seven Bridger Mountain populations varied from 0.9 to 3.2 km^2. Winter home ranges averaged 0.8-5.0 km^2 (Pac *et al.* 1991). Migratory whitetail females inhabiting coniferous forest had home ranges averaging only 0.6-0.7 km^2 in summer (Leach 1982, Morgan 1993) and less than 0.3 km^2 in winter (Mundinger 1982). In the prairie-badlands environment, migratory female mule

deer had home ranges averaging 2.1-2.9 km^2 in summer and 2.3-3.4 km^2 in winter, compared to an overall average resident home range of 6.3 km^2 (Wood *et al.* 1989). White-tailed deer exhibited individual movement patterns ranging from small, stable home ranges to erratic shifts within very large home ranges in prairie-agricultural habitat. Thus, home ranges averaged 3.3 km^2 in summer and 6.3 km^2 during winter within an overall average home range of 33.5 km^2.

Direct comparisons of average home range sizes for deer in environments we studied and other areas were hampered by differences in methods and sample sizes among studies. Despite this limitation, our estimates for the two species, both sexes, and various environments fell within the range of home range sizes reported elsewhere (Wood 1987). Largest and most variable home range sizes occurred among mule deer and white-tailed deer in prairie-badlands and prairie-agricultural environments. Smallest average sizes and least variability was evident in relatively diverse, stable riverbottom and montane forest environments.
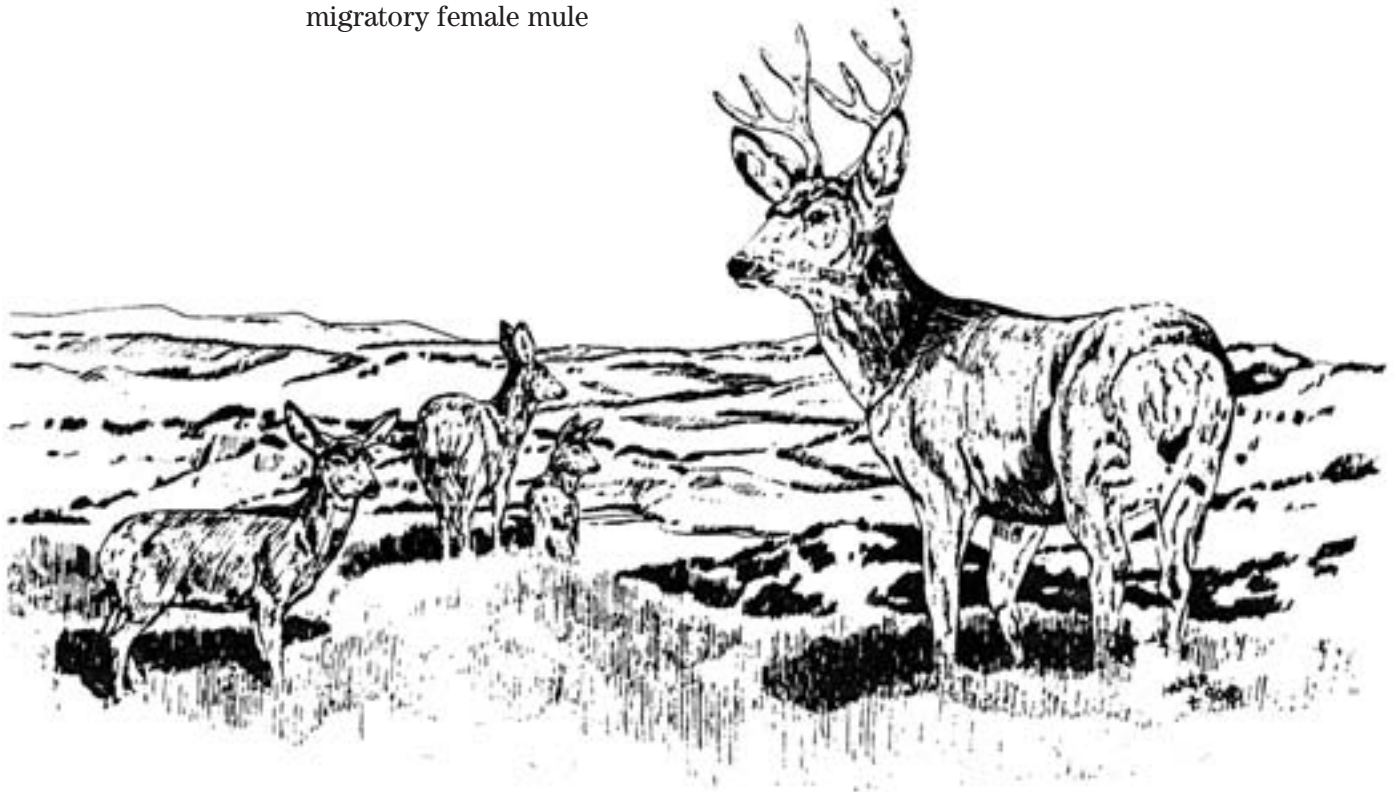
Selection and Use of Vegetation

In conjunction with other habitat components, especially topography, vegetation helped structure the landscape and provide the physical and biotic environment deer required to inhabit an area. Habitat diversity, influenced by topographical and/or vegetational diversity, appeared to be a good indicator of intensity of deer use. In mule deer habitats, vegetational diversity usually followed topographic diversity, thus topographic diversity may be the major or ultimate factor influencing mule deer use of an area (Hamlin and Mackie 1989).

In white-tailed deer habitat, vegetational structure and other physical site factors promoted diversity. Overhead cover and mesic areas were available to some extent in all areas occupied by white-tailed deer. Compton *et al.* (1988) reported a direct relationship between the amount of riparian cover and abundance of white-tailed deer. Whitetails were more commonly associated with agricultural lands than were mule deer.

Across the state, results indicated that selection and use of vegetation was driven by habitat structure. At the local level, specific vegetation types or plant species were important in use patterns. However, specific plant types and species were only part of the environmental complex involved in providing for the forage, spatial isolation, cover, and other needs of deer.

Where available, mule deer selectively used structurally diverse forest vegetation, especially for reproductive habitat. Nonetheless, this apparent preference was invariably tempered by selection for other site factors, especially topographic diversity. In non-timbered breaks, badlands, and other prairie environments, topographic characteristics and variation appeared to become more important, if not the driving force in habitat selection.

In the Bridger Mountains, multilayered, low- to medium-elevation conifer stands in conjunction with topographic diversity provided a wide array of succulent, high quality forage throughout the parturition-lactation period (Pac *et al.* 1991). Perhaps equally important, these stands also provided isolation from other deer, security from predation, and avoidance of competition from other wild ungulates (e.g. elk) and livestock. Topographic diversity, which included variation in slope, exposure, and elevation, also was important in providing diverse microenvironments and cover types that supplied a varied and long-lasting source of quality forage. As Klein (1985) also noted, maximization of selective foraging is most likely to occur in mountainous regions where variability in exposure, slope, and altitude create a diversity of microclimatic influences.

Structurally complex and diverse vegetation not only met all requirements for reproduction, but also met them better on more restricted areas. Thus, home ranges were smaller, and greater numbers of individual parturition territories were supported in any given area or unit of habitat. Conversely, extensive areas of gentle to moderate slopes dominated by open shrub-grass vegetation or dense, even-age conifer forests were avoided or used as maintenance habitat by males and nonproductive females.

In the Missouri River Breaks, reproductive habitats were more structurally diverse than maintenance or unused habitat (Hamlin and Mackie 1989). Habitats used more heavily by deer exhibited greater numbers of patches and diversity of cover types than areas that were unused or used only occasionally. Mule deer used areas containing forested cover types more during all seasons than expected based on availability. Selection for diversity was also evident in their preference for areas with four or more locally interspersed cover types and at least moderate topographic relief. Patches of Douglas fir-juniper and scattered-moderate density ponderosa pine-juniper-grass cover were most strongly selected. Conclusions about the overriding importance of any specific type(s), however, must be tempered by the fact that Douglas fir types were distributed only over the western portion of the area; deer on the

Habitat diversity appeared to be a good indicator of intensity of deer use.

eastern portion did not have the option to select fir, and had to choose from pine-juniper and other less preferred types.

In timbered breaks, as in the mountains, structurally diverse timbered types plus topographic variation provided the highest quantity and quality forage, the greatest opportunity for extending selective foraging through the lactation period, spatial isolation for productive females, hiding cover for fawns, and the least opportunity for interspecific competition with elk and livestock. Expansive ridgetop and coulee-bottom areas dominated by open low shrub-grassland vegetation were avoided, especially by lactating females.

Selection of winter maintenance habitat in the Missouri River Breaks was even more strongly related to topography and structure of vegetation. Douglas fir types received more use than during other seasons. Areas of low relief, even when timbered, were vacated as snow accumulated and weather conditions became severe. Under such conditions, moderately steep terrain that included both open or semi-open south-facing slopes and moderate to dense timber on northerly exposures combined to provide

the physical conditions deer needed to survive.

Habitat selection and use of vegetation in prairie-badlands environments also was strongly related to topographic characteristics. On the Cherry Creek study area, extensive open rolling mixed-grass prairie was avoided (Wood *et al.* 1989). Badlands and mesic hardwood draws were selected and used heavily throughout the year. Interspersion of hardwood draws and badlands provided the resources required by mule deer throughout the year. Hardwood draws were the primary source of succulent forage and dense hiding cover during fawn rearing and comprised both reproductive and yearlong habitat for adult females. Because of the lineal nature of the draws, most females isolated themselves on fawning territories spaced along the length of draws in suitably structured habitat. When badlands and hardwood draws were lacking, mule deer were dispersed widely and exhibited greater variability in use of vegetation.

On sagebrush grassland prairie in northeast Montana where hardwood draw vegetation was lacking, mule deer occurred widely spaced as individuals

or small groups along narrow, sharply cut drainageways that dissected the area (Jackson 1990). These cuts provided some succulent vegetation as well as daytime cover. During summer, deer moved to adjacent uplands or creek bottoms where they foraged selectively through the night before returning to the cuts at dawn. Use of all vegetation cover types on the area, except for very limited creek bottoms, generally corresponded to availability. This included the extensive big sagebrush-grassland type, which covered 64 percent of the area and seasonally accounted for 38-59 percent of the total use of vegetation cover types.

Patterns of habitat/vegetation use documented that mule deer can adapt successfully to most environments in Montana. Occurrence of alfalfa and yellow sweetclover that provided succulent, high quality forage during summer and autumn or small grain and other croplands that provided high energy forage in autumn and winter stimulated mule deer use of areas that otherwise might be unused or used only occasionally.

Mule deer near Colstrip responded positively to vegetation and other habitat changes associated with strip-mining

and reclamation as well as to forage and cover resources available within the city (Fritzen 1995). Because of restricted hunting, the deer were highly acclimated to the presence and activities of humans and utilized all available habitat and vegetation resources present. In autumn and winter, deer made heavy use of fruits and other forages available from gardens and landscaping in the city. Some deer adapted a strongly nocturnal activity regime while others acclimated to the presence of people and were active throughout the day. In adapting to the presence and activities of humans, deer benefitted not only from the resources available but also the reduced threat of predation.

White-tailed deer occur almost exclusively in association with riparian or mesic upland vegetation that provide overhead cover or with agriculture. They also are associated with gently rolling topography with slopes less than 30 degrees. Dry, topographically diverse upland environments that lacked riparian vegetation or agriculture were selected almost exclusively by mule deer.

In summer, vegetation selection by white-tailed deer, especially reproductive females, appears to be driven by needs

for high quality forage, isolation, and security in association with overhead cover. Environments that structurally provide for all three are selected irrespective of the specific vegetation cover types represented. Similar environments lacking in one or more serve as maintenance habitat for males and/or nonproductive females. On the lower Yellowstone River, productive adult females used mature cottonwood stands more heavily than bucks and unproductive females during spring and summer. Although whitetails are generally considered most adapted to early successional vegetation, mature cottonwood exhibited the highest total nutrient load among all seral communities on the area (Boggs 1984).

At the landscape level, habitat selection by whitetails in northwestern Montana was constrained by elevation as well as by vegetation, roads, riparian areas, slope, and aspect (Morgan 1993). Preferred habitats occurred below 1,525 m; habitats above about 1,650 m were avoided. The preferred elevational range spanned all major creek bottomlands and adjacent drainages and slopes and included the major riparian, meadow, and lower elevation forest habitats used by white-tailed deer. When the influence of elevation was removed, vegetation was an important factor in habitat selection.

Perhaps the most distinctive feature of vegetation use by whitetails across all study areas was the preference exhibited for diversity, both structural and vegetational, associated with riparian habitat. Summer distribution in the Salish Mountains (Morgan 1993) and Swan and Clearwater River Valleys (Leach 1982) centered in riparian-meadow habitats along major river valleys, creek bottoms, and associated drainageways. Diverse upland timbered types associated with riparian habitats provided additional resources and allowed individuals to meet their needs throughout spring, summer, and autumn. Higher elevation areas that whitetails avoided were further from major riparian areas and lacked the diverse vegetation associated with the lower, preferred habitats (Morgan 1993).

Riparian habitats were particularly important in spring and early summer. However, as vegetation in these habitats matured, deer moved upward from wet bottomlands to mesic timbered types that provided quality forage and cover during late summer and autumn.

The marked preferences of white-tailed deer for diverse forest cover associated with riparian habitats also was apparent in winter. Winter maintenance habitats selected by whitetails were characterized by interspersion of timbered riparian areas and diverse, subclimax coniferous forest habitat types. These habitat complexes, located in foothill and lower valley areas, provide overhead cover to maintain the snow and thermal conditions whitetails require while also providing opportunities for deer to forage. Open, logged, and agricultural habitats that accumulated deep snow were essentially unused except under mild conditions or in proximity to human developments.

In semiarid eastern Montana, white-tailed deer occur primarily in association with riparian vegetation along rivers, streams, and other mesic drainageways. Locally, they also occur in association with agricultural and ponderosa pine habitats (Allen 1971, Swenson *et al.* 1983, Dusek 1987).

A yearlong preference for mesic ponderosa pine habitat types in the Long Pines in southeastern Montana was similar to use of conifer-dominated habitats in northwestern Montana. Selection of hardwood draw and agricultural communities adjacent to the pine uplands during spring-autumn allowed females to isolate themselves and maximize their intake of succulent forage during fawning. Strong selection of the pine community in winter, especially severe winters, may have reflected the overriding value of thermal cover and energy conservation when agricultural fields and other habitats were of limited value to deer.

Whitetails on Yellowstone River bottomlands selected habitats with relatively large amounts of riparian cover. Patterns of habitat selection and

reproductive output by adult females suggested that reproductive habitats on the lower Yellowstone were characterized by comparatively high diversity and interspersion of riparian communities and agriculture (Dusek *et al.* 1989). Selection and use of agricultural fields by does with fawns increased from mid-June to September. Selection of agricultural lands at night increased from summer to winter. Summer habitats used by males and nonproductive females included more stream bed, young riparian forest, and agriculture than habitats used by productive females.

Deciduous riparian forest and shrub habitats that whitetails used in winter provided little thermal cover for energy conservation. However, the availability of agricultural forages allowed deer to range widely and forage selectively to maximize intake and maintain a favorable energy balance during cold periods even when feeding at night in open environments.

White-tailed deer in prairie-agricultural environments also selected riparian areas. However, habitat diversity and interspersion of cropland and rangeland also influenced deer use (Dusek *et al.* 1988). On the Cherry Creek area, whitetails preferred hardwood draws throughout the year while agricultural and most rangeland types received minor use (Wood *et al.* 1989). Hardwood draws interspersed in badlands decreased winter home range size and provided the only shelter available during severe winter conditions. Only rough badlands and mixed-grass habitats were consistently avoided.

Forage Selection and Use

As noted earlier, mule deer and white-tailed deer are adapted to selectively forage on plant materials that are low in cellulose and high in cell soluble proteins, carbohydrates, and fats (Hanley 1984, Hudson 1985, Putman 1988). These adaptations mandate that deer seek high quality, easily digested plant materials throughout the year. Our studies suggested that the importance of

foraging adaptations has been underrated in evaluating deer-habitat relationships.

On most of our study areas, and especially in nonagricultural areas of eastern Montana, high quality forage was relatively patchy while moderate to low quality forage was typically abundant. Deer often were forced to be opportunists, foraging selectively on the best of what was available when and where it was available. Forage selection varied temporally and spatially within and among study areas. Food habits and foraging patterns also varied among individuals, sex and age classes, and species (Figs. 20 and 21).

The composition of deer diets reflects availability of vegetation types and plant species occurring within home ranges. Because of variation in nutrient and other chemical characteristics, use of individual plants can vary greatly. What is selected in one area at one time may be avoided or utilized at a different time in another area.

Collectively, our data on food habits supported the conclusions of Coblentz (1970) and Suring and Vohs (1979) that deer prefer green herbaceous forage. Browsing occurs extensively only in absence of green herbaceous forage, although leaves and fruits of numerous

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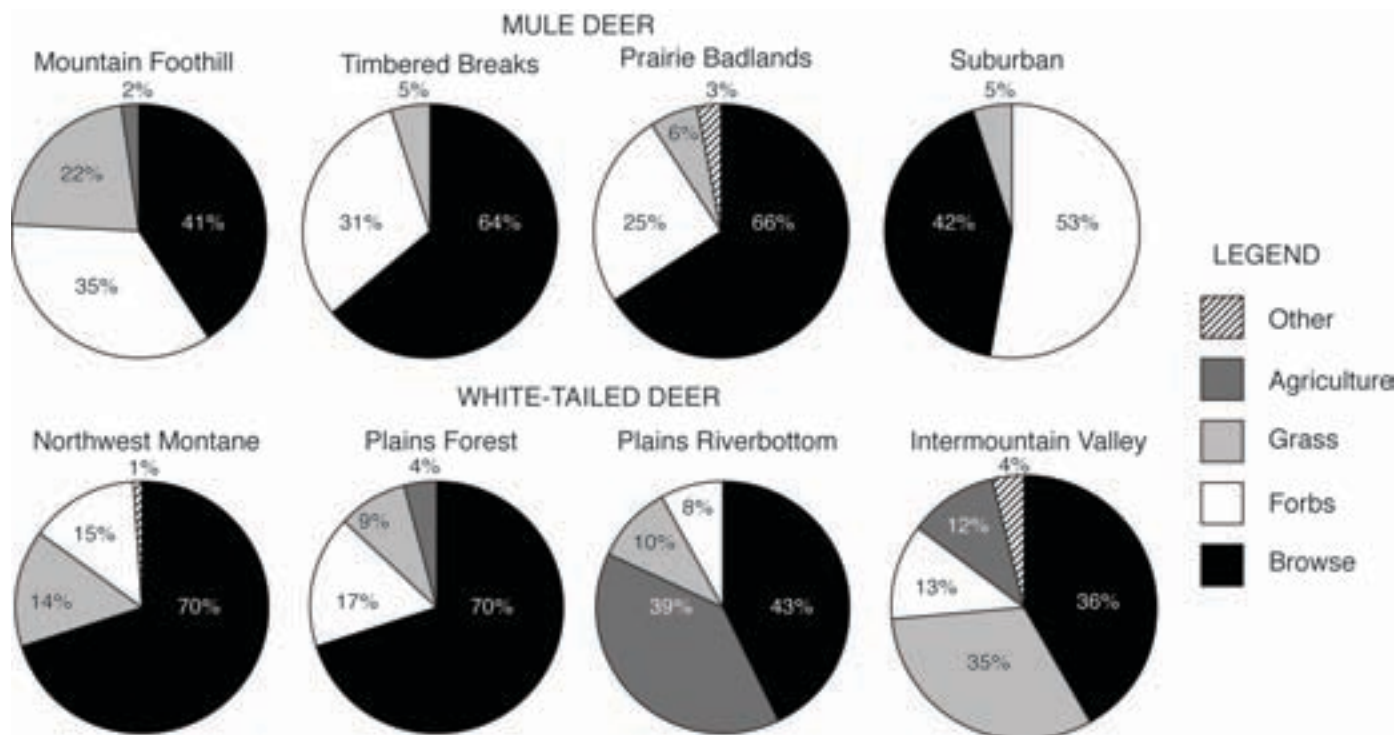
Figure 20.
Generalized yearlong use of forage classes of mule deer and white-tailed deer in different environments.
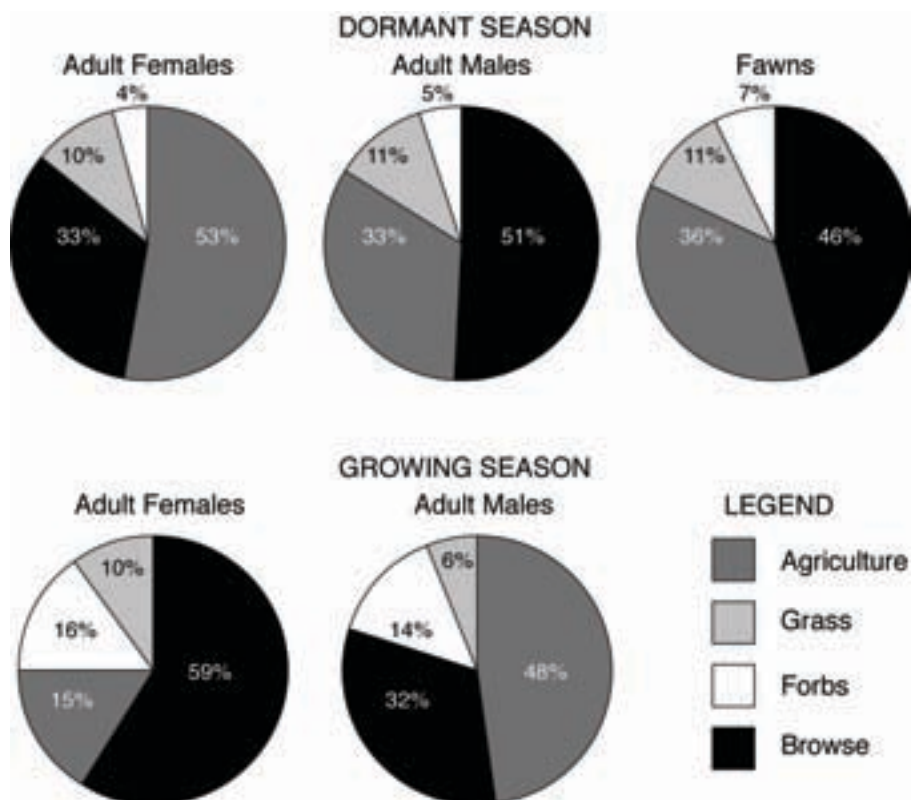
Figure 21.
Use of forage classes by fawn, adult male, and adult female white-tailed deer on the lower Yellowstone River during periods of vegetative growth and dormancy, 1980-86 (Dusek et al. 1989).

shrubs and trees contribute importantly to summer and autumn diets in most areas. Extensive browsing on twigs, evergreen leaves, and conifer needles occurs primarily in autumn, winter, and early spring when green forage is unavailable.

Summer diets of mule deer in the Bridger Range were dominated by forbs, while browse and grasses received moderate and minor use, respectively (Pac *et al.* 1991). During autumn, diet composition was highly variable, but shifted toward browse. Use of grasses and sedges increased. In winter browse predominated followed by grasses and forbs. During spring, mule deer made increased use of grasses and forbs. Use of agricultural crops and products was generally low and only local.

Annual food habits of mule deer in timbered breaks paralleled those of deer in the mountain-foothill environment. Some seasonal differences in use of forage classes occurred as a result of wide fluctuations in forage availability between seasons and years in the Missouri River Breaks (Hamlin and Mackie 1989). Shrubs accounted for an average 36 percent of the diet from May through July and 50 percent or more of monthly diets during August-March. Peak use of shrubs occurred in December and January. Forbs comprised one-third or more of the forage used from April through September, with highest use during May-July, when they accounted for 60-70 percent of the diet. Lowest use of forbs occurred in December and January, coincident with greatest use of browse. Use of grasses was relatively minor, with peak use from late March through April and, in some years with autumn greenup during October and November. Availability of agricultural crops was very limited and local throughout the breaks.

Studies in prairie environments also indicated variability in forage selection in relation to local environmental characteristics and land uses (Dusek 1975, Jackson 1990, Fritzen 1995). In prairie environments, shrubs comprised over 50 percent of the diet during all seasons and up to 96 percent in winter (Dusek 1975, Jackson 1990). Use of

forbs was moderate, typically peaking in June and declining in relation to availability thereafter. Use of grasses was minor and followed seasonal trends similar to those in the timbered breaks environment.

On the Colstrip area that included ponderosa pine, disturbed and revegetated areas, local agricultural fields, and urban habitats, herbaceous plant materials were relatively abundant and available during all seasons. Use of forbs exceeded that on other areas, reaching 88 percent in summer, more than 50 percent during autumn and spring, and 16 percent in winter (Fritzen 1995). Use of grass was minor, with peaks in spring and autumn.

White-tailed deer in northwestern Montana were primarily browsers during summer and autumn (Morgan 1993). Grass and grasslike plants were selected in addition to browse in spring, while forbs accounted for most of the non-browse forage in summer and autumn. Grass, typically found in greater abundance in riparian areas, made up a substantial portion of the diet only in spring when use of these habitats was greatest. Riparian meadows and adjacent open to diverse upland forest habitats also provided forbs and browse plants during late spring and early summer. As meadows and other low elevation sites began to dry and forage plants matured, deer moved to higher elevation forest habitats. Concurrently, deer shifted their diets from grasses and forbs to browse. Agriculture was limited throughout the forested mountain valley region so crops were used only locally.

Along the lower Yellowstone River in eastern Montana, food habits of white-tailed deer were influenced by the relative abundance and variety of agricultural crops as well as the natural forage available (Dusek *et al.* 1989). Browse (43 percent) and agricultural crops (39 percent) dominated the yearlong diet (Figs. 20 and 21). Forbs were important and received moderate use only in summer, while grasses received moderate use in spring. Use of agricultural crops was important during all seasons, but was

minimal in May and June and peaked in autumn. Alfalfa was the primary species used during summer while row crops and small grains were selected in late autumn and winter. However, differences in availability influenced forage selection spatially along the riverbottom. The importance of agricultural crops surpassed browse where alfalfa or other crops were readily available. Availability of crop residues also varied in relation to irrigation and other cropping practices.

Composition of the diet of white-tailed deer in the Long Pines reflected their preference for ponderosa pine habitats. Pine habitats were characterized by high diversity and abundance of low growing shrubs, and browse was strongly selected in all seasons. Forbs were most abundant and received moderate use in spring and summer, with declining use in autumn and winter. Grasses received moderate use in spring and autumn. Agricultural crops were used by some deer that moved daily from uplands to bordering agricultural fields. Alfalfa was selected in spring, wheat and barley in autumn.

Like other attributes of habitat use, food habits reflected a high degree of selection of plant materials available to individuals. Each deer selected the best of what was available within its home range. Both behavior and resource requirements motivated habitat and food selection.

Activity Patterns

We were able to monitor detailed activity patterns by direct observations of deer and the activity and distances traveled by radio-collared deer during 24-hour tracking sessions. A more generalized index to changes in activity and mobility was gathered from measuring the average distances traveled by radio-collared deer on a monthly basis. The two approaches helped gauge how deer were exploiting their habitat and why they were employing a particular combination of activities in various environmental settings.

The general pattern of deer activity during a 24-hour period includes major peaks of activity near sunrise and sunset (Fig. 22). This bimodal pattern is generally characteristic of both species of deer inhabiting a broad spectrum of environments. However, deer are capable of considerable adjustment in activity patterns as they adapt to local environmental conditions.

The most distinct feature of daily activity patterns of white-tailed deer on the lower Yellowstone was movement between woody cover and agricultural fields. Daily activity of whitetails along the lower Yellowstone River during summer included very sedentary use of riparian cover during daytime, restricted movement to nearby alfalfa fields before sunrise, and greater movement and more intense use of alfalfa fields after sunset (Fig. 22).

Daily activities of adult females during summer were influenced by their reproductive status. Non-producing females made greater use of agricultural fields during June-mid August while does with fawns were largely sedentary in riparian cover. By early September, use of agricultural fields by productive does had risen to levels similar to nonproductive females.

During winter, daily patterns included greater activity and mobility associated with more intense nocturnal use of agricultural fields (Fig. 22). Deer often traveled 2-2.5 km to feed in fields located some distance from riparian cover. Whitetails usually returned to the same daytime bedding and loafing areas even though other cover was available near the fields being used at a particular time. During winter, deer activity within cover patches used during daylight hours was much greater compared to summer and involved longer bouts of feeding on native riparian forage.

Ambient temperatures had a decided effect on daily activity, but this relationship varied among the different environments occupied by deer. During summer on the lower Yellowstone River, whitetail activity in midday was significantly lower at temperatures above than below 32° C. This relationship reversed one hour after sunset with
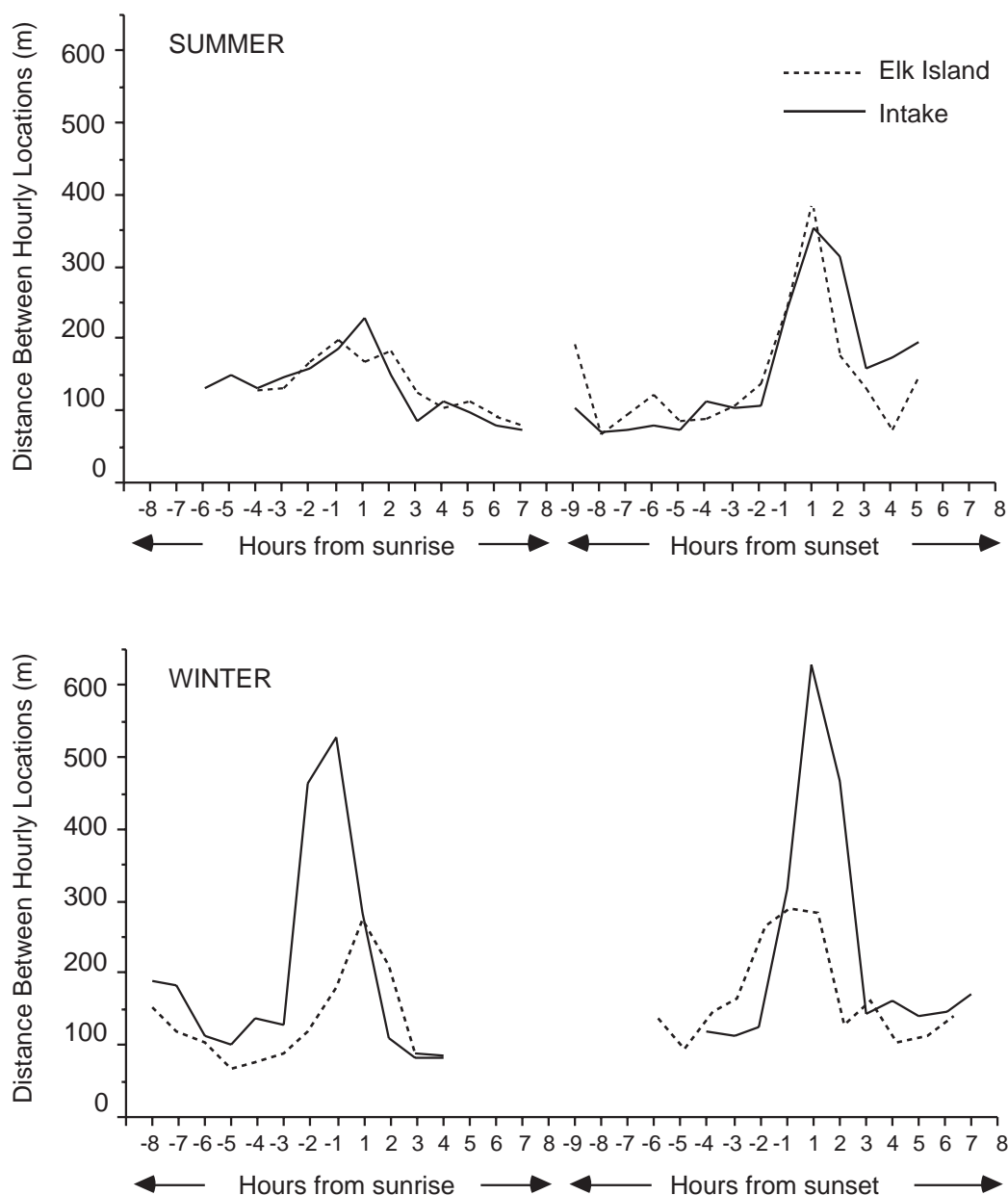
Figure 22.
Mean distances moved between successive locations of deer during 24-hour tracking sessions through summer and winter on the Elk Island and Intake units along the lower Yellowstone River (Dusek et al. *1989).*

greater movements observed at higher than lower temperatures.

During winter when whitetails had access to crop residues and maintained a high nutritional plane, they continued to exploit agricultural fields even when wind chill temperatures dropped to -60° C. With low temperatures and high winds deer might be expected to select microsites with lower wind speeds within a field such as along edges or ditch banks, but this was not observed for whitetails along the lower Yellowstone (Herriges 1986).

In contrast, Wood (1988) reported that ambient temperature and the effects of wind chill significantly influenced winter habitat use and daily activity of mule deer occupying native prairie-badlands habitat. Wind was a constant factor in this environment, averaging 21 km/hr during 57 random measurements. Over a normal winter ambient temperature range of -24° to 11° C, deer avoided windy sites at wind speeds greater than 10 km/hr. By use of shelter associated with badlands topography, mule deer reduced conductive heat loss

by 47 percent at feeding sites and by 61 percent in bedding sites. Energy gained from native forage offset the energy lost from increased exposure and mobility associated with feeding only when conditions were relatively mild (Wood 1988). Foraging was energetically inefficient during severe winter weather conditions. Bedding in protected sites was the favored strategy because it conserved energy.

Adjustments in activity also were made in response to different types of human disturbance. Vogel (1983) concluded that deer activity during daylight hours decreased with increasing levels of human disturbance. Whitetails inhabiting more developed areas became increasingly nocturnal and secretive and made greater use of cover during the day. Herriges (1986) indicated that agricultural fields in close proximity to human disturbance did not receive diminished use by white-tailed deer. However, most of the deer activity in those fields occurred during hours of darkness in both summer and winter. Fritzen (1995) described nocturnal movements by mule deer that exploited seasonally available forages associated with landscape plantings within the city limits of Colstrip. Compton (1986) reported that whitetails made greater use of larger tracts of riparian cover in

Whitetails inhabiting more developed areas became increasingly nocturnal and secretive ad made greater use of cover during the day.

the river bottom or moved into adjacent uplands during mid-late autumn. This shift coincided with firearm hunting seasons, introduction of cattle onto the river bottom, sugar beet harvesting, and social behavior of deer during the rut.

During all seasons, whitetails on the lower Yellowstone River made disproportionately heavy use of areas where cattle were absent, although use of these areas often involved only minor shifts in activity and distribution. Avoidance of cattle may reflect either alteration of food and cover (Mackie 1978) or a social intolerance (Lonner 1975). The latter was apparently of greater importance along the lower Yellowstone River because deer vacated an area as soon as cattle arrived and returned to the grazed areas when cattle departed (Compton 1986).

Telemetry tracking during 24-hour periods on some of our study areas provided a better understanding of how nocturnal activity influenced our interpretation of movement patterns and home range size. Herriges (1986) and Dusek *et al.* (1989) reported that nighttime activity associated with movement out of large blocks of riparian cover to agricultural fields increased seasonal home range size 2-3 fold compared with daytime ranges. This dichotomy in habitat use tended to occur

in environments where preferred bedding and foraging sites were spatially distinct.

Jackson (1990) described day and night differences in activity patterns for mule deer occupying native ranges in open sagebrush/grassland habitats. He reported that deer were highly active and moved extensively at night. Summer home ranges based on combined day and night locations of radio-collared deer were 105-934 percent larger than those based only on daytime locations. One mule deer doe used totally different areas during each of three 24-hour tracking sessions; and none of these areas overlapped the home range polygon plotted from daytime locations (Fig. 23). These extended nocturnal movements were associated with deer that spent daytime hours in shale hills and at night traveled to drainage bottoms and reservoir areas where succulent forage was available.

Other female mule deer on Jackson's (1990) study area showed much less dichotomy in day and night habitat use. Home ranges calculated from daytime locations were similar in size to areas used during both diurnal and nocturnal periods (Fig. 24). Deer with relatively small home ranges occupied diverse sites

that satisfied all resource requirements. However, these individuals represented a small proportion of the total population in this rather simple, open environment.

Dichotomy between areas used through the day was less evident for deer occupying diverse timbered habitats. Morgan (1993) reported that white-tailed deer in northwest Montana made somewhat greater use of small, open meadows at night. However, these meadows usually occurred interspersed with other foraging sites, security cover, and bedding areas within small seasonal home ranges. Daily travel between bedding and foraging areas was minimal, and other patterns of habitat use were more subtle than those in more open environments. The luring influence of agricultural crops and proximity to high levels of human disturbance was generally absent for whitetails in montane forests of western Montana. Because of this, data collected only during daylight hours may be more representative of overall habitat relationships for deer in those areas than in open or patchy environments with significant human disturbance and agriculture.

Changes in monthly activity and mobility provide a generalized indicator
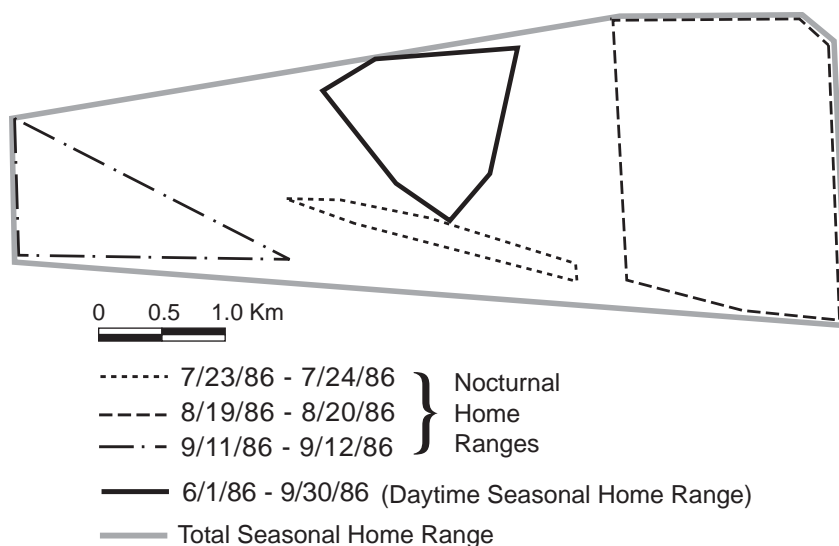
Figure 23.
Nocturnal home ranges compared to daytime and total seasonal home ranges of one radio-collared female mule deer during summer on open sagebrush-grassland habitat, northeast Montana (after Jackson 1990).

Deer No. 1187

Deer No. 1087

Deer No. 1287

| 0 | 0.5 | 1.0 km |

```
----------  7/23/86 - 7/24/86  ⎫ Nocturnal
- - - - - -  8/19/86 - 8/20/86  ⎬ Home
-·-·-·-·-·-  9/11/86 - 9/12/86  ⎭ Ranges

───────     6/1/86 - 9/30/86 - Daytime Seaonal Home Ranges

━━━━━━      Total Seasonal Home Range
```
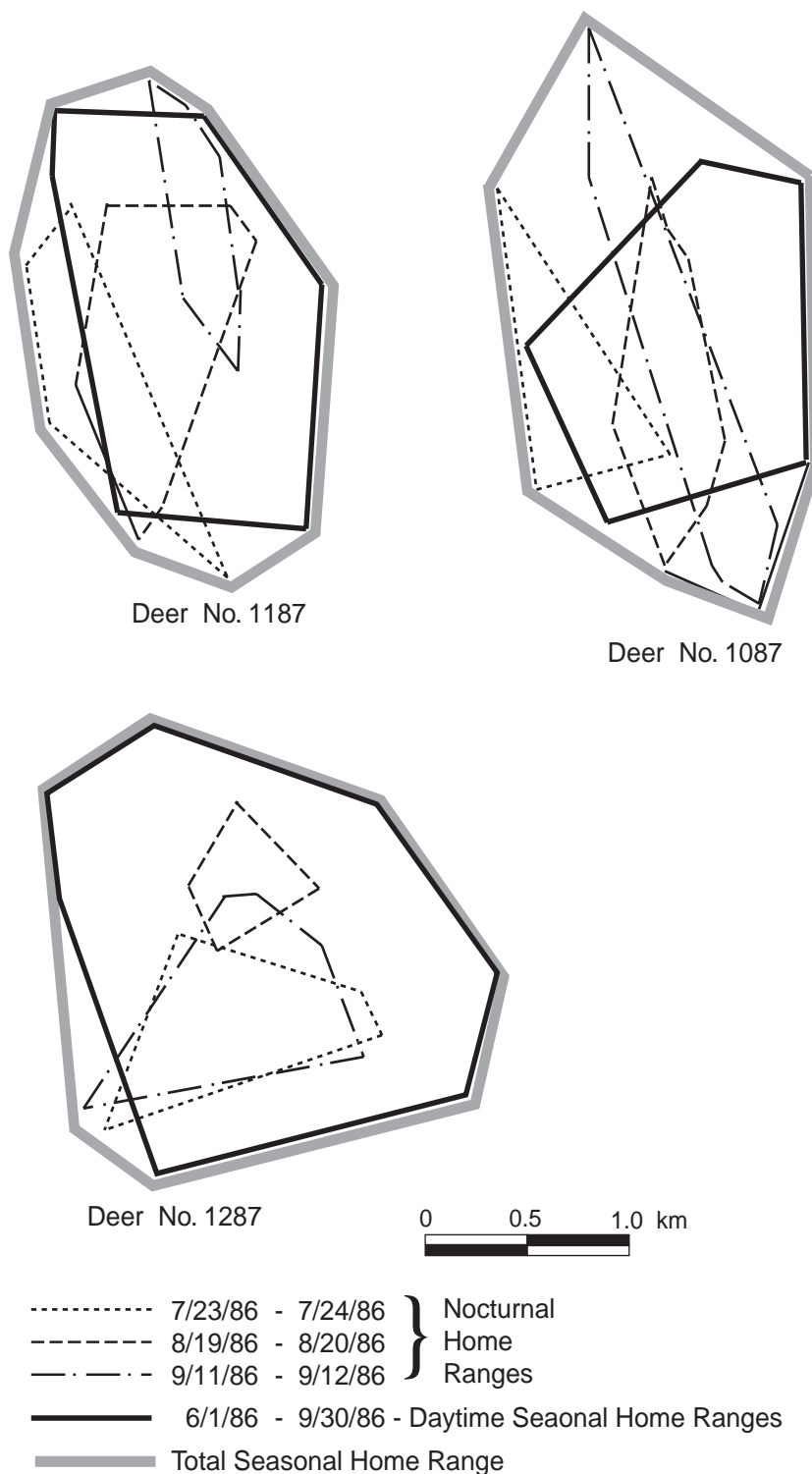
Figure 24.
Nocturnal home ranges compared to daytime and total seasonal
home ranges of three radio-collared female mule deer during
summer on open sagebrush-grassland habitat, northeast Montana
(after Jackson 1990).

of adjustments in the overall strategy of habitat use by deer during the biological year (Dusek *et al.* 1989, Hamlin and Mackie 1989, Pac *et al.* 1991). For example, average activity radii for radio-collared adult female mule deer in the Bridger Mountains show annual trends in mobility for mule deer in different environments (Fig. 25). Differences in physical and vegetative characteristics of east and west slope winter ranges resulted in divergent patterns of mobility and activity.

During winter and spring mule deer on the east slope of the Bridger Range exhibited significantly higher mobility. In this open, dry environment deer remained widely distributed across large areas consisting of shrub-grassland and some dryland agricultural fields. Such dispersion seemed to favor efficient allocation of forage. Even under severe weather conditions, the overall winter strategy continued to emphasize high mobility to access available forage on widely separated, windblown ridges. On the west slope, very low mobility during the winter months (Fig. 25) was consistent with a strategy that favored energy conservation (Youmans 1979) through a winter period that averaged 40 days longer on the west as compared with the east slope.

The spike in mobility that occurred for deer on the east slope during April and May was related to their earlier departure from winter ranges and greater distances traveled en route to summer ranges. On the west slope, deer left winter ranges later, and distances traveled to summer range were shorter. However, migratory movement extended into June because of the high elevation habitats that were exploited.

Trends in mobility among deer in the two environments converged during June-August (Fig. 25). This was associated with fawn-rearing requirements and the sedentary behavior of deer on summer home ranges. Such a convergence in habitat use would likely occur when resource conditions were most favorable and deer preferences could be fully expressed even in very different environments.
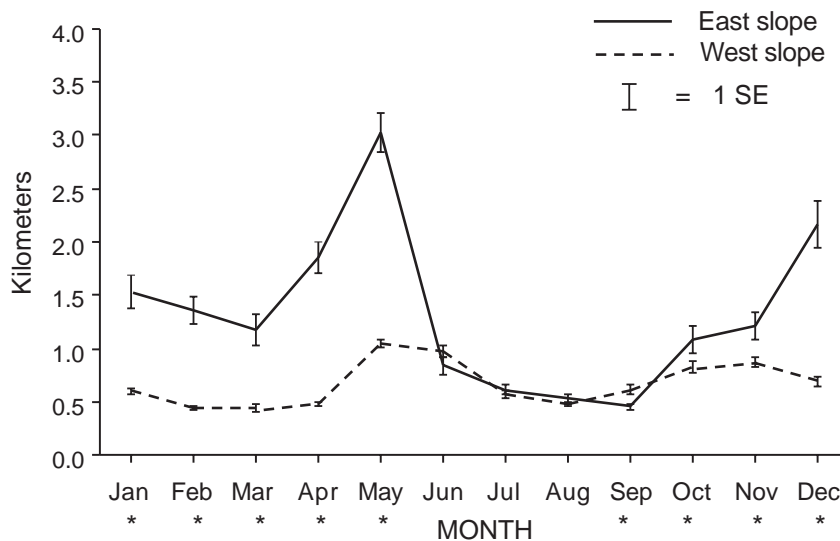
Figure 25.
A comparison of mobility based on monthly average activity radii (km) for adult female mule deer on the west and east slopes of the Bridger Mountains. Asterisk indicates significant differences between areas P < 0.05, one-way ANOVA (after Pac et al. *1991).*

Changes in mobility and strategies of habitat use occurred again in September when some west slope deer responded to early autumn snowstorms by crossing the Bridger Divide in early movement toward winter range. However, deer on the east slope exhibited greater mobility during October-December as increasing numbers of deer moved long distances toward winter ranges. West slope deer completed movement toward winter ranges during October and November, and by December mobility was limited in the manner characteristic of winter. Annual differences in autumn movements and mobility appeared to be influenced primarily by weather patterns, though rutting behavior and hunting probably had some effect.

Comparisons of data collected on deer study areas across the state indicated that adult females demonstrated very similar low levels of mobility during the summer fawn rearing period regardless of species and the type of habitat occupied (Dusek *et al.* 1989, Wood *et al.* 1989, Hamlin and Mackie 1989, Pac *et al.* 1991). In contrast, winter mobility patterns were more divergent, reflecting differences in characteristics of local environments and the specific behavioral and biological strategies required to exploit them.

Social Organization

As discussed earlier, many attributes of social behavior are common to both mule deer and white-tailed deer. Interaction between behavior and resource requirements produced an array of strategies by which individuals of both species exploited various environments. Social relationships are never static because the environments deer inhabit and the manner in which deer use them are constantly changing. In spite of this, members of established populations function in an orderly manner.

Social organization depends on individual recognition and established patterns of communication between sex and age classes. It functions to minimize tension among individuals, contributes to efficient allocation and use of habitat, and enhances survival and reproductive fitness among members of the population. Much of this is accomplished through adjustments in the size and composition of social groups and their spatial distribution across the landscape.

We distinguished four types of social groups. Doe groups include at least one adult (1 year or older) female but no mature (2 year and older) males. Buck groups consist of at least one mature male but no adult females. Mixed groups contain both adult does and mature bucks. Yearling male groups include at least one yearling male with no adult does or mature bucks. Doe, buck, and mixed groups may include fawns and/or yearling males. However, in the Missouri River Breaks, buck and most mixed groups of mule deer usually did not contain fawns (Hamlin and Mackie 1989). After antler shedding in February, the identity of the four social groups cannot be distinguished reliably until antler growth resumes in late-May and early June.

Social organization in both species centers around maternally-related doe groups.

Social organization in both species centers around maternally-related doe groups. The other three social group types are of secondary importance in occurrence and persistence. In most environments, composition and size of mule deer doe groups was determined primarily by reproductive effort and success.

During June and July, the majority of does were either solitary or with newborn fawns. This occurred on all study areas regardless of topographic and vegetative structure. Fawns, the age class most vulnerable to predation, occurred in the smallest social groups widely distributed across all available reproductive habitat.

Hamlin and Mackie (1989) reported that does without fawns joined other nonproductive does rather than remaining solitary during early summer. Female groups were largest when reproductive success was lowest, and vice versa.

The size of mule deer doe groups in the Bridger Mountains gradually increased during August-October (Fig. 26) as fawns were weaned and began to travel routinely with the doe. Groups consisting of two or more does with their fawns also became more common as maternally-related females regrouped. During the entire summer-early autumn period fewer than 5 percent of all adult females occurred in groups with mature males (Hamlin and Mackie 1989, Pac *et al.* 1991).

Doe groups declined in size somewhat in November with the onset of the rut. Courtship and bucks chasing does in estrous apparently contributed to temporary disruption of social groups. Disturbance during the hunting season may also have disrupted social organization, resulting in smaller group size.

As autumn progressed toward winter, forage desiccation and snow accumulation became primary influences on habitat use, overriding behavioral preferences for small group size and maximum dispersion. Size of doe groups increased sharply from November through January as deer became restricted to winter maintenance habitats (Fig. 26).

In many populations, social affiliation and size of buck groups was undoubtedly minimized by high

Number of Groups
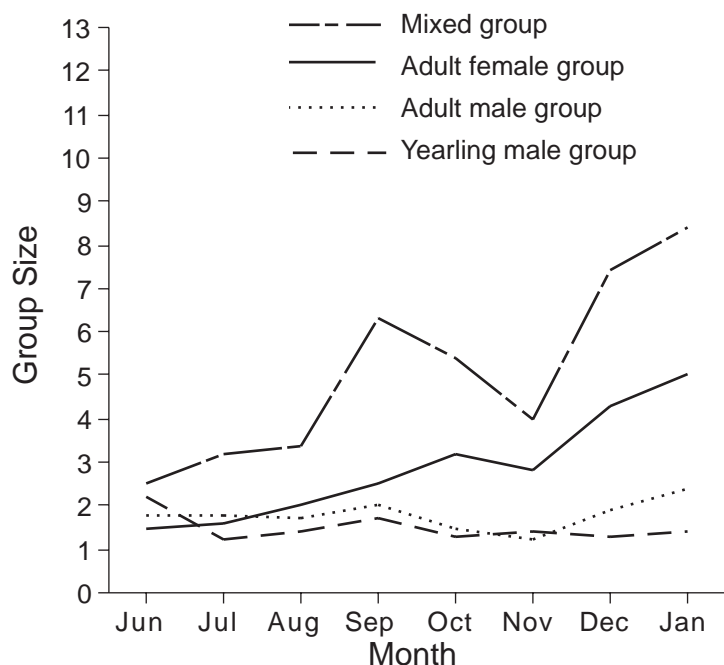
	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan
Mixed group:	4	13	18	3	8	20	136	167
Adult female group:	194	390	402	240	185	136	744	1127
Adult male group:	36	160	236	58	34	23	70	137
Yearling male group:	4	44	33	19	10	10	20	26

Figure 26.
Monthly mean size of four social groups of mule deer on the west slope of the Bridger Mountains (after Pac et al. *1991).*

hunting mortality. Mule deer buck groups averaged about 2.0 during June-September on the west slope of the Bridger Mountain Range (Fig. 26), and only about 20 percent of all buck groups contained three or more males (Pac *et al.* 1991).

Buck groups were smallest in November during the rut when most mature bucks were alone or in mixed groups. Association between mature bucks and yearling bucks reached a minimum during the rut (Pac *et al.* 1991, Hamlin and Mackie 1989). Based on observations of marked males, Hamlin and Mackie (1989) reported that size of mature buck groups in winter-spring was equivalent to summer.

Mixed groups were temporary associations that occurred in relation to specific activities or in response to environmental factors. Mixed groups in the Bridger Mountains were uncommon during June-October when does sought isolation to raise fawns and bucks associated with one another (Fig. 26). Observations of mixed groups increased in November with the onset of the breeding season and peaked in December-January when weather conditions forced deer to congregate on limited winter habitat. During all months mixed groups were the largest of all group types.

Yearling male groups were temporary affiliations because individual members preferred to associate with adult females or mature bucks whenever tolerated. On the west slope of the Bridgers, yearling male groups averaged 1-2 individuals in all months during June-January (Fig. 26). Yearling males increasingly associated with adult females as the biological year advanced while association between yearling and mature bucks peaked during July-September and declined thereafter (Hamlin and Mackie 1989, Pac *et al.* 1991).

Relationships concerning group composition and size for mule deer in the Bridger Mountain Range and Missouri River Breaks generally apply to both species in other environments (Wood 1986, Dusek *et al.* 1989). Greatest differences among populations involved group sizes during winter and spring. The largest groups tend to occur in mountainous habitat where snow accumulation forces migratory deer to congregate loosely on small, sparsely timbered winter ranges. In other areas, deer may temporarily aggregate in large groups to exploit high quality food resources. On the west slope of the Bridger Mountain Range, group size was largest in spring, averaging 11 deer/group with 27 percent of all groups consisting of 10 or more deer (Pac *et al.* 1991). Group sizes also peaked during spring in the Missouri River Breaks but averaged only 4.5 deer/group (Hamlin and Mackie 1989).

Results of our studies showed that sex and age classes occurred not only in different social groups, but also in separate areas during much of the year. Segregation of the sexes was apparently the end result of a number of interacting factors. As discussed earlier, the peak energetic investment in the reproductive effort by the two sexes occurs at different times during the year; each with a corresponding set of physiological consequences. Efforts to meet these different reproductive roles begin far in advance of the actual events when resource requirements unique to each sex result in preference for habitats with different characteristics. Habitat partitioning among does and bucks was most evident during the fawn-rearing period in summer when sexual segregation was reinforced by aggression of maternal does toward other deer.

Figs. 27 and 28 present two examples of social distribution at widely separated points along the environmental spectrum in Montana. The high degree of topographic and vegetative diversity in the Bridger Mountains (Fig. 27), provided ample opportunity for habitat partitioning among the primary social groups during fawning.

Aggressive behavior by maternal does resulted in efficient allocation of diverse montane forest habitats among the female segment. It also enforced the segregation of mature bucks, yearling males, and unproductive females into

Results of our studies showed that sex and age classes occurred not only in different social groups, but also in separate areas during much of the year.
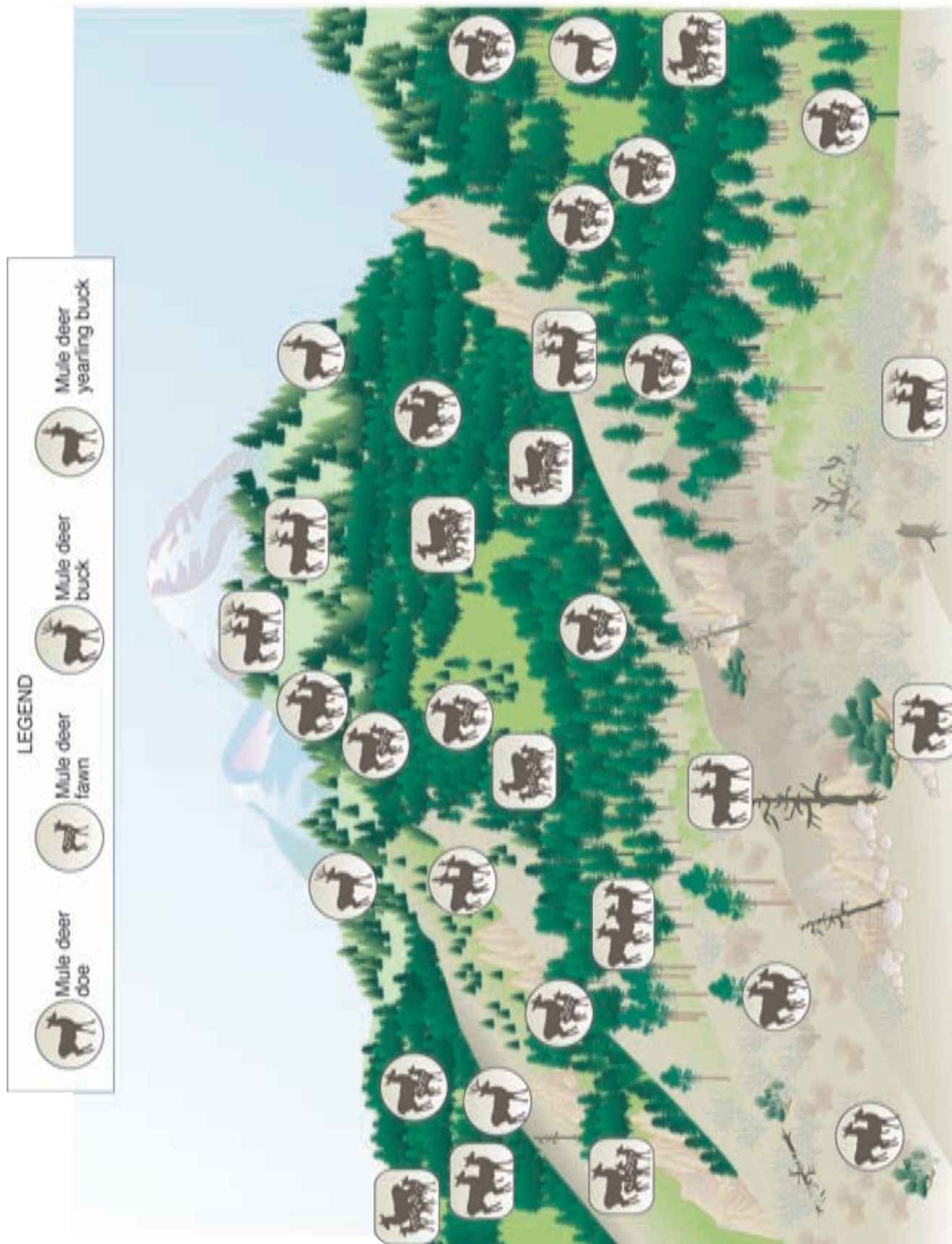
Figure 27.
Spatial segregation of social groups of mule deer at fawning time (mid-June) in the Bridger Mountains.

LEGEND

White-tailed doe

White-tailed fawn

White-tailed buck

White-tailed yearling buck

Figure 28.
Spatial segregation of social groups of white-tailed deer at fawning time (mid-June) along the lower Yellowstone River:

adjacent remaining habitats with different characteristics. Mature bucks could satisfy their requirements for large quantities of forage in more open, less secure habitats within the subalpine zone, along drier ridge tops within the montane forest, or on low elevation winter maintenance habitats. Unproductive does and yearling males also utilized these habitats as well as portions of the montane forest that were not occupied by maternal does.

The mosaic of topography and vegetation along the lower Yellowstone River was far more subtle than that in the Bridger Mountains. Consequently, habitat partitioning by white-tailed deer occurred at a finer scale (Fig. 28), although its functional significance in providing social organization and allocation of habitat was similar. The distribution of all social groups on the lower Yellowstone River at fawning time revolved around the preference of maternal females for mature cottonwood and green ash stands. These structurally diverse habitats provided the greatest concentration of forage and cover. The greatest number of fawning territories used by maternal does occurred in these communities situated adjacent to irrigated agricultural crops. Moderate numbers of maternal females were associated with mature cottonwood stands on islands and bottomlands lacking agricultural fields. Limited numbers of does and fawns utilized open, upland agricultural areas interspersed with hardwood draws.

Groups of mature whitetail bucks were distributed along the interface between mature cottonwood stands and dry badland bluffs and in young cottonwood stands along the river's edge. Bucks also occurred in the interior of mature stands of cottonwood wherever use by maternal does was limited. Unproductive does and yearling males were generally distributed in willow thickets along the river, in open agricultural areas, and along hardwood draws that traversed the dry terraces adjacent to the riverbottom.

Population Characteristics and Dynamics

The Concept of Population

The concept of "population" is fundamental to the field of ecology. However, no single definition is widely accepted, and biologists often use the term only vaguely to designate any group of individuals of the same species.

Some ecologists conceptualize a population as a discrete biological or ecological unit. For example, Nicholson (1957) proposed that population be defined as "a group of interacting and interbreeding individuals that normally has no contact with other groups of the same species...that is to say...a discrete dynamic unit." Such populations may be selected for adaptation to the specific environments in which they live (Mayr 1970), an interpretation that also can connote a "deme" (Gilmour and Gregor 1939).

Nelson and Mech (1987) suggested that white-tailed deer associated with individual winter yards in northeastern Minnesota comprised behaviorally separate "subpopulations" that constituted genetic demes. They hypothesized that deer populations may consist of conglomerates of subpopulations or demes. Groups of subpopulations occupying discrete patches of habitat also have been termed "metapopulations" (Gilpin and Hanski 1991, Hunter 1996).

Generally, in all existing definitions, the essential criteria for conceptualizing or designating a population are species, group, and space. More recently,

interbreeding and other elements of genetics have become important. Although Nelson and Mech (1987) and others have implied a relationship between a deer population and its environment through social organization, no one directly links habitat and population in their definition. Thus, none of the existing definitions for population completely described the deer population-habitat relationship we observed.

Based on behavioral responses associated with habitat selection and use, we distinguished mule deer and white-tailed deer populations as relatively discrete, dynamic units. However, we also expanded this definition to imply behavioral and biological adaptation to the habitat(s) in which deer occur. A similar view has been expressed by Lidicker (1994, 1995) with respect to distribution and abundance of mammals in general. Ostfeld (1992) also indicated that the community context of a population is an essential aspect of its functioning and we cannot expect to understand populations independently of this context.

In our perspective, a deer population consists of an assemblage of individuals and family groups bonded together by traditional distribution, movement, and other habitat use patterns within a discrete unit of habitat. As described earlier, they are established and maintained through social organization and behavior inherent to a matriarchal society. Lifelong fidelity of individual female deer and their offspring to seasonal ranges ensures some continuity of basic distributional patterns through time. Further, it ensures continued population unity as a group of partially interacting and interbreeding individuals. Based on this, the term "population" is no longer a conceptual abstraction (Pac *et al.* 1991). Yearlong distribution of each population delineates the complete ecological unit required to sustain it. Physical and biotic characteristics of the habitat determine the strategies that can be successfully employed by members of the population to effectively occupy and maintain themselves in that environment

In our perspective, a deer population consists of an assemblage of individuals and family groups bonded together by traditional distribution, movement, and other habitat use patterns within a discrete unit of habitat.

over time. Both environment and strategy influence deer demographics and dynamics.

Our concept of population as a discrete behavioral, biological, and ecological unit was supported by patterns of population development and growth observed or inferred for mule deer. We speculate that development of deer populations follows a predictable pattern from initial colonization through the various stages of habitat exploitation and population growth. It also was possible to conceptualize additional categories or levels of organization below and above the population.

Colonization and Development of Populations

Development of a new deer population in any environmental complex entails:

- colonization by pioneering individuals
- population growth and spread through reproduction, dispersal of young females, and behavioral adaptation to fill all available reproductive habitat
- behavioral fine-tuning, including habitat partitioning and modification of distribution, movements, and other habitat use for optimal exploitation of the area.

Colonization of vacant habitat by females primarily involves young adults dispersing from natal home ranges and emigrating from natal populations. Such movements typically occur during late spring-early summer when adult females aggressively defend their fawning territories and force some yearlings to leave the maternal range. At this time, environmental conditions are most benign and provide dispersing young deer with the best conditions for traversing unfamiliar terrain and relocating outside the maternal home range.

Successful early colonists select home ranges that meet all of their

resource needs for survival and reproduction. Because all habitats are potentially available, some emigrants will settle in areas unsuitable for survival. Females that localize in areas which function both as winter maintenance and reproductive habitat would meet their needs and be afforded the greatest probability of survival. These deer and the habitat complexes they occupy become the nuclei for expansion of fledgling populations. Yearlong residency, which requires minimal specialization in seasonal movement and habitat use, may be a fundamental strategy for successful pioneering and colonization.

Growth and development of colonizing populations requires continued recruitment and dispersal of young females to additional habitat. Although foothills and other low elevation habitats often provide sufficient resources for winter survival of large numbers of deer, local areas capable of providing succulent forage and other resources essential for successful reproduction by adult females may be limited. This minimizes the number of generations of females that can establish home ranges near resident matriarchs and results in dispersal of some juvenile females to adjacent areas.

In mountain ranges, young females seeking summer home ranges find extensive areas of mesic habitat in montane forests at middle elevations above the foothill zone (Pac *et al.* 1991). Although montane forests may provide plentiful reproductive habitat, snow limits use in late autumn and winter. This requires movement to lower elevations in autumn and the establishment of separate winter home ranges. If these winter ranges overlap the area on which the deer had ranged as fawns, they also serve to maintain the linkage between related females and fawns through the habitat they occupy. This seasonal association of maternally-related females on specific portions of winter range probably fosters behavioral accommodation of increasing

numbers of deer on limited winter maintenance habitat. It also gives social organization to the developing/expanding population as an array of family groups comprised of related females and offspring.

Exploitation of montane forest habitats, at least initially, requires only moderate specialization. The distance separating seasonal ranges is slight and migration involves only simple, up-down movements. However, as reproductive habitat at middle elevations adjacent to foothills becomes filled by adult females and their offspring, dispersing juvenile females from both foothill and adjacent montane forest habitats must travel further and adopt more complex movement and habitat use patterns. Habitats available at this time may be located primarily above the montane forest, in more distant forests across high mountain divides, or in patchy, low-elevation environments. Use of such habitats requires greater specialization in movements and habitat use.

This increasingly complex distribution and movement pattern permits members

Once pioneering is accomplished, a successful colonist probably employs a fundamental strategy of yearlong residency.
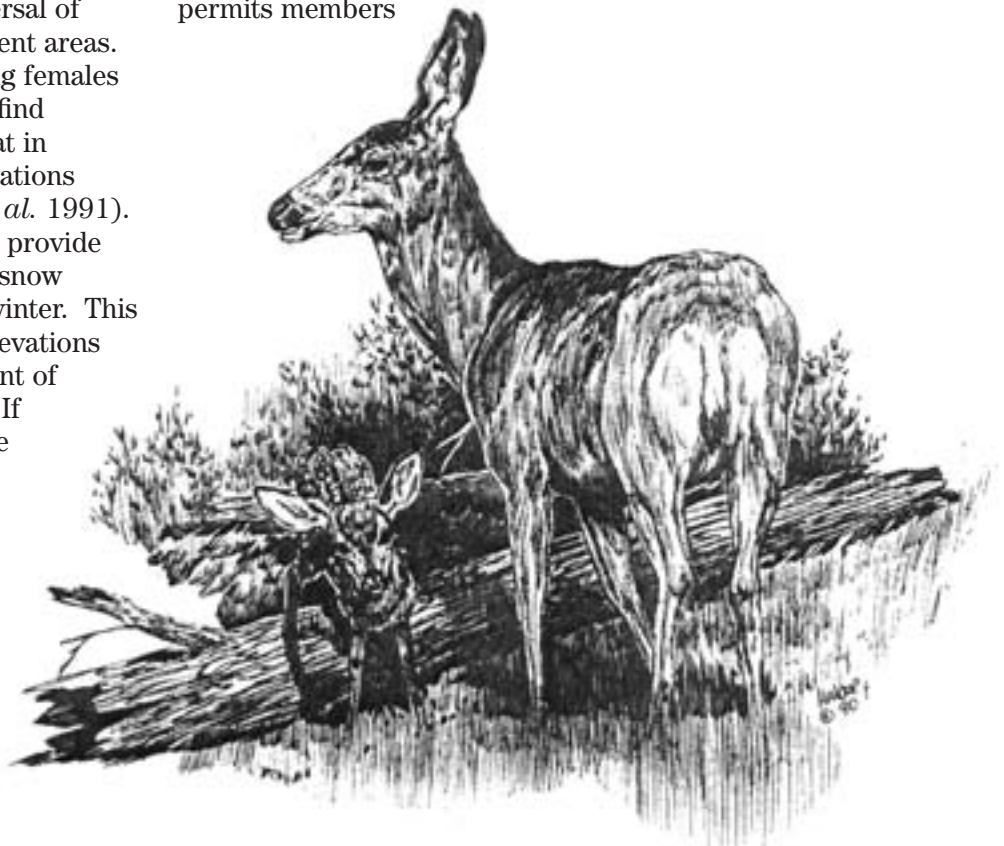
of developing populations to exploit all habitat capable of supporting reproduction in a particular location. Ultimately population expansion and growth become limited as individuals encounter environmental barriers or compete for space and other resources with deer from other developing populations. Such barriers and areas of overlap form the boundaries between habitats used by deer from adjacent populations in the Bridger Mountains (Pac *et al.* 1991). Movement beyond the boundaries usually results in emigration to different populations rather than long-distance movement within the same population.

Successful patterns of habitat use become traditional and transmitted from generation to generation through the long-lasting social bonds of matrilineal groups.

Successful patterns of habitat use become traditional and transmitted from generation to generation through the long-lasting social bonds of matrilineal groups. This process provides for continued efficient exploitation of available habitat. It also assures that boundaries between habitats used by individual populations and other natural groupings of deer are maintained.

High rates of recruitment, dispersal, and establishment of young females in vacant habitat are associated with eruptive population growth following colonization. When most or all reproductive habitat is filled, habitat partitioning becomes increasingly important, and young deer are forced to use lower quality, maintenance habitats available within that population-habitat unit. In some habitats this may also lead to other behavioral adaptations and more refined use of space and resources by all deer.

Colonization and selection of habitats by males followed a different pattern. The social bond between young male mule deer and their mothers weakens earlier, and some leave family groups prior to the onset of fawning (Hamlin and Mackie 1989). In our studies, mule deer dispersed from spring through autumn. Most yearling male whitetails spent summer on the periphery of natal home ranges and dispersed during late autumn. Most yearling males in both species dispersed from natal home ranges and some left natal populations permanently.

Young males of both species can readily colonize vacant habitats because of their propensity to disperse from natal home ranges. Most males of both species eventually established home ranges within distributional perimeters previously established by females of the populations. This concurred with Porter *et al.* (1991) that males add little to spatial expansion or overall distribution of populations.

Data for mule deer in the Missouri River Breaks suggest that recovery of populations after periodic declines follows a pattern similar to initial colonization and development. Following severe population declines, spatial distribution of females centers in "core" areas that meet all requirements for survival under the most extreme environmental conditions. Core areas are local habitats with optimal mix and juxtaposition of both winter maintenance and reproductive habitat. They tend to be surrounded by areas of decreasing habitat quality and declining deer use. Deer occupying such core habitats are primarily residents.

In the Missouri River Breaks, high recruitment and pre-saturation dispersal led to rapid filling of core habitat throughout the area (Hamlin and Mackie 1989). As these habitats filled with mature females, young does were increasingly forced to use lesser quality

reproductive and maintenance habitats. These usually were smaller patches with less topographic and vegetational diversity than core habitats. They were also subject to greater fluctuation in environmental conditions, offered less security from predators, and increased opportunity for competition with livestock and other wild ungulates. Use of these habitats often resulted in larger home ranges, distributional shifts that included seasonal use of accessory areas, and migrational movements similar to patterns observed in mountain environments.

Although we speculate recolonization proceeds similarly to initial colonization, social behavior of deer in river breaks and prairie-badland environments displayed greater plasticity than in mountain-foothill habitats. Dispersal rate of young females was greater than in the mountains, perhaps because important habitats occurred in smaller patches and/or average recruitment rates were higher. Further, it appeared that dispersal was adaptive and resulted in rapid fill and complete use of all available habitat in these environments. Once populations were established, high rates of dispersal were less important in complex mountain environments.

Population Organization

Mule deer in the Bridger Mountain Range provide a graphic example of population organization in the species, at least for mountain-foothill environments. We recognized a series of five natural groupings of increasing complexity among mule deer inhabiting the Bridger Range (Fig. 29).

The most fundamental unit was the matriarchal family group (Fig. 29A). Aggregations or loose bands of matrilineal groups and attendant buck groups associated with specific units of habitat appeared to constitute local subpopulations (Fig. 29B) (Youmans 1979, Pac *et al.* 1991). In winter, these groups used overlapping home ranges on restricted winter maintenance habitat.

Under severe conditions and in early spring, they often shared common range areas but avoided mixing with groups of deer associated with adjacent winter habitat. In late spring, subpopulation identity became blurred as individuals and groups used overlapping movement corridors and summer home ranges that radiated outward from each segment of a particular winter range.

Overlapping subpopulations associated with a definable unit of habitat comprised population-habitat units (Fig. 29C) (Pac *et al.* 1991). The existence of seven distinct population-habitat units in the Bridger Range was related to the occurrence of discrete areas of winter maintenance habitat around the perimeter of a long, narrow strip of diverse reproductive and summer maintenance habitats. Each population-habitat unit comprised a discrete unit from the standpoint of mule deer distribution, habitat use, demographics, and dynamics (Pac *et al.* 1991). This concept does not require total spatial separation or physical isolation of populations and some overlap of individuals from adjacent population-habitat units commonly occurred along the boundaries between units.

Higher levels of population organization in the Bridger Mountains were defined by genetic sampling of mitochondrial DNA (Cronin *et al.* 1991) as well as other aspects of biology, behavior, and demographics (Pac *et al.* 1991). Those data suggested that the four adjacent population-habitat units on the east slope of the Bridgers comprised a single deme (Fig. 29D), or the largest community of potentially interbreeding individuals within a generally similar and continuous environment (Gilmour and Gregor 1939). A separate and distinct deme included the three population-habitat units along the western portion of the Bridger Range (Fig. 29D). Movements, including dispersal patterns of young deer, indicated interchange of animals occurred primarily among adjacent population-habitat units within demes. Dispersal across the Bridger Divide to another deme was limited almost entirely to young males.
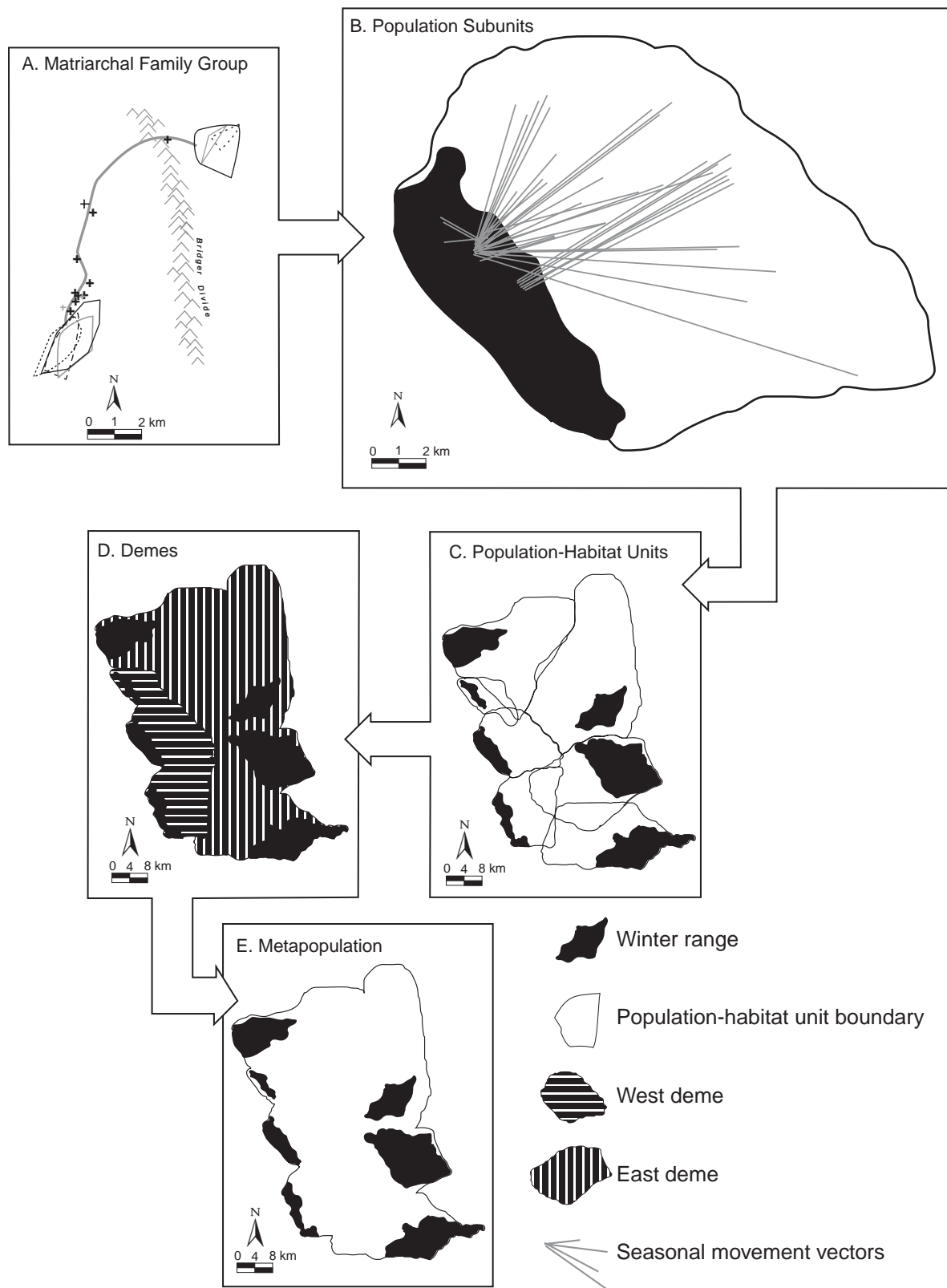
Figure 29.
Five levels in a series of natural grouping of mule deer in the Bridger Mountains.

At the highest level of organization, the two adjacent demes separated by a major landscape discontinuity may represent a single Bridger Mountain "metapopulation" (Fig. 29E). Hanski and Gilpin (1991) and Hunter (1996) defined a metapopulation as a "population of populations."

The same organizational relationships may have characterized natural groupings of mule deer in timbered breaks and prairie-badlands environments. However, the broad expanse and subtle changes in environmental characteristics across the northern plains made it difficult to define units at the population and higher levels of organization. Winter maintenance habitats were more diffuse or patchy and often located within yearlong home ranges (Fig. 7). They did not necessarily form nuclei for development and recognition of organizational units as in the mountains. Instead, population structure centered in matriarchal groups and subpopulations consisting of loose aggregations of those groups and associated males.

In prairie environments, spatial distribution and movement patterns allowed recognition of matriarchal groups associated with core areas that included both reproductive and maintenance habitats for all members of the group. Loose aggregations of deer within specific geographic portions of the area formed more or less discrete subpopulations. In these environments, intensive radio-tracking studies, similar to those on our Bridger Mountain and Missouri River Breaks study areas, may be necessary to define population-habitat units and higher levels of organization. We had confidence in describing organization only through the subpopulation level.

In eastern Montana, white-tailed deer along the lower Yellowstone River apparently comprised a population distinct from whitetails occupying adjacent prairie-agricultural and timbered upland environments (Dusek 1987, Dusek *et al.* 1988, Dusek *et al.* 1989, Wood *et al.* 1989). Within the riverbottom, subpopulations were associated with particular segments of floodplain (Dusek *et al.* 1989). These exhibited differences in demographics and dynamics similar to differences exhibited by mule deer in different population-habitat units in the Bridger Mountains. However, the continuous yearlong distribution made it impossible to clearly delineate discrete populations. Studies in other areas show that contiguous subpopulations of white-tailed deer exhibiting different demographics and dynamics also are genetically separate units (Manlove *et al.* 1976, Ramsey *et al.* 1979, Rhodes and Smith 1992, Scribner 1993).

Population Characteristics

Our studies characterized populations of both species across much of the broad spectrum of environments they encounter in Montana. From a landscape perspective, each study area and deer population was characterized by demographics unique to the environment in which it occurred. The more alike the environments, the more similar the populations were in demographic characteristics and dynamics.

Population Size and Density

Population size and density have been used interchangeably. Population size refers to the total number or estimated number of deer in a population at a given time; density is the number of deer per unit area. Population size is finite; density is relative, but it is the parameter most used when comparing deer numbers among areas of different size. Deer density is far from uniform across environments. Density distribution varies widely between seasons in some environments, but it changes only slightly in others.

Measurement and comparison of deer densities also is hampered by topographic variation in land surface per unit map area. For example, a square kilometer of steep, rugged mountainous terrain may include 10 percent more area than a square kilometer of moderately dissected breaks and 20-30 percent more surface than the same area of level to rolling prairie. In addition, nearly all habitat complexes include some proportion of unused area or rarely used habitat which can be difficult to delineate without intensive study.

In our studies, the amount, quality, and distribution of reproductive habitat appeared to be the primary factor influencing density distribution and potential total numbers of productive adult females in each population. The mix of food, cover, and water available in reproductive habitats determined the minimum home range size needed by individual females. The total amount and quality of reproductive habitat determined how many home ranges or adult females each area could support. Complex, diverse environments capable of providing optimum resource availability allowed females to attain comparatively high densities. Such environments often included adjacent habitat for young adult females and adult males that resulted in larger overall populations. Use of patchy, variable environments characterized by reduced or unpredictable resource availability was associated with greater movement, larger home ranges, and lower overall densities.

Winter maintenance habitat appeared to exert less influence than the total amount and quality of reproductive and summer maintenance habitat on population size or overall density of deer. This does not negate the overall importance of winter maintenance habitat to occurrence and abundance of deer. The existence of deer populations depends on availability of areas that ameliorate adverse effects of deep snow, provide shelter from extreme temperatures, and

...the amount, quality, and distribution of reproductive habitat appeared to be the primary factor influencing density distribution and potential total numbers of productive adult females in each population.

provide escape cover from humans and other predators. Also, high quantity and quality of winter forage supplemented and reduced the rate of utilization of energy reserves. However, deer are adapted to tolerate restricted distribution and high densities during winter. Therefore, total numbers of deer in a population reach levels dictated by the quantity and quality of available summer habitat, rather than winter maintenance habitat.

Varying quantity and quality of summer habitats resulted in differences in numbers of deer associated with winter ranges. Those numbers could not be directly correlated with kinds and amounts of winter forage or other attributes of winter ranges.

Comparisons of mule deer numbers and density among populations in the Bridger Mountains exemplify these relationships. Total deer numbers and density were not necessarily related to size of the population-habitat unit (Pac *et al.* 1991). For example, the large number (~2,100) and high average density (6.7/km^2) of deer in the Brackett Creek population reflected occurrence of large units of high quality reproductive habitat directly adjacent to a large area of winter-maintenance habitat (Fig. 30A).

Conversely, the Battle Ridge population occupied the largest area of any population. It included a large amount of winter range that sustained only a modest population (~850) at low average density (1.4/km^2). That low density reflected large amounts of unused habitat and only limited reproductive habitat distributed predominantly in patches around the periphery of the unit (Fig. 30B).

Hamlin and Mackie (1989) reported an average population of about 1,000 mule deer on the 275 km^2 Missouri River Breaks study area during winters 1960-1987. Annually, however, populations varied widely from a low 390 (1.4/km^2) in spring 1976 to highs of about 1,700 (6.2/km^2) in autumn 1983 and 1987. During spring, density averaged 3.0 (1.4 to 4.5) mule deer/km^2. Both the mean and range of densities in the timbered breaks fell within the lower end of the range of densities recorded for populations in the Bridger Mountains.

Densities recorded for mule deer populations on open prairie-badlands habitat were even lower, ranging from 0.6 to 2.0/km^2 on the Cherry Creek study area (Wood *et al.* 1989) and 0.9 to 2.0/km^2 on the Dog Creek study area in northeastern Montana (Jackson 1990). Densities in

Varying quantity and quality of summer habitats resulted in differences in numbers of deer associated with winter ranges. Those numbers could not be directly correlated with kinds and amounts of wnter forage or other attributes of winter ranges.

*Figure 30.
Comparison of
distribution of
reproductive and
maintenance habitats
and unused areas in
Brackett Creek (A)
and Battle Ridge (B)
population habitat-
units in the Bridger
Mountains (after Pac
et al. 1991).*

Reproductive

Maintenance - summer

Maintenance - winter

Unused

A

N

0   2   4 km

B
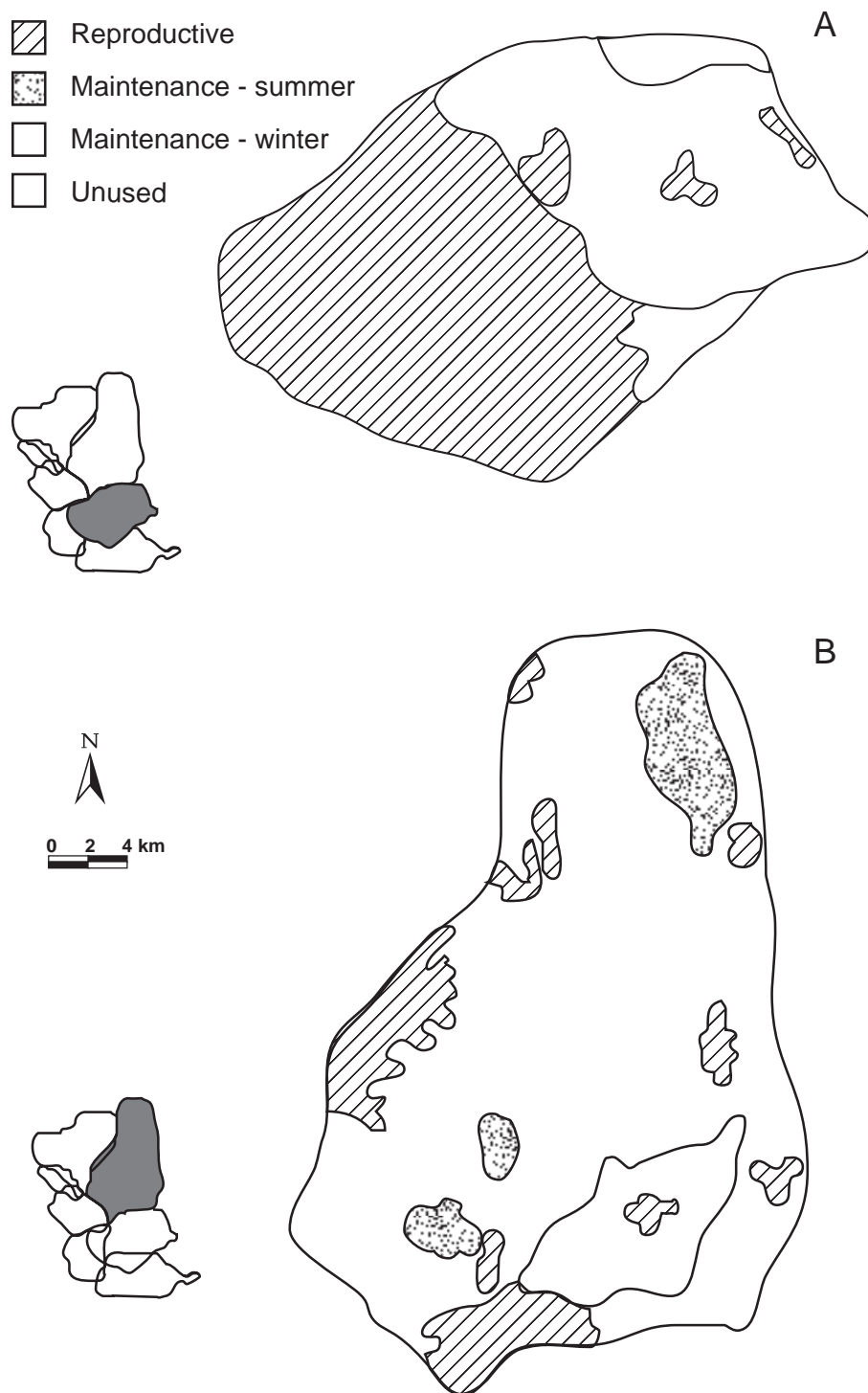
both of these areas fell within the range
of densities calculated for mule deer in
hunting districts across southeastern
Montana (0.1-3.3/km², Youmans and
Swenson 1982) and non-timbered breaks
habitat adjacent to Tiber Reservoir in
northcentral Montana (0.7-4.4/km², Olson
1986).

Relatively high densities were
sometimes observed for mule deer in
environments influenced by agriculture
and other human activity. Winter densities
ranging from 5 to 10 /km² (ave =7/km²)
and 3 to 14/km² (ave. = 8/km²) have
been reported for non-timbered breaks-
agricultural habitat along the Coffee

Creek-Arrow Creek and Sage Creek-Indian Creek drainages, respectively, in central Montana (Stivers, pers comm.). Similarly, Fritzen (1995) found an average 7.5 mule deer/km^2 in a plains population inhabiting a surface mine-reclamation-suburban habitat complex in the vicinity of Colstrip in southeastern Montana.

For white-tailed deer, total numbers and densities in riverine environments varied directly with amount of riparian forest and shrubland cover along the bottomlands (Compton *et al.* 1988). Occurrence of riparian habitat interspersed with agriculture and rangeland also strongly influenced white-tailed deer distribution, habitat use, and apparently their abundance on upland prairie-agricultural habitats (Dusek *et al.* 1988).

Highest whitetail densities were recorded along the lower Yellowstone River. Riverine environments like bottomlands of the Yellowstone River today represent habitats of relatively high complexity, diversity, and stability (Dusek *et al.* 1989). Complexity and diversity are provided by interspersion of relatively small units of many different vegetation cover types, land uses, and agricultural

practices. Stability is inherent in the sense that availability of vegetative resources is high and predictable over time within small, local areas. Densities varied from <15/km^2 to >50/km^2, in accord with amount of riparian cover and other characteristics of bottomlands (Compton *et al.* 1988, Dusek *et al.*1989). By comparison Hamlin (1979, 1980) reported minimum densities of 6-12 whitetails/km^2 on unfarmed bottomlands along the Missouri River. Because tree and shrub components were similar to the lower Yellowstone, density differences between the two areas might be attributed to the lack of agriculture and interspersion of crop and riparian components along the Missouri River.

Lowest average density of whitetails was recorded in prairie-agricultural habitat on the Cherry Creek study area, where densities peaked at <0.6/km^2 overall and 5/km^2 on local areas (Wood *et al.* 1989). Estimates based on modeling of harvests and age structures in the Swan Valley (Riley pers. comm.) suggested maximum average densities of about 5-6 white-tailed deer/km^2 of yearlong habitat.

Within study areas, density distribution of deer varied seasonally in

For white-tailed deer, total numbers and densities in riverine evironments varied directly with amount of riparian forest and shrubland cover along the bottomlands.

response to changes in environmental conditions influencing quantity and quality of habitat available and the annual cycle of deer behavior. In mountain-foothill habitats, deer were widely distributed in summer and early autumn and became increasingly aggregated during late autumn, winter, and early spring. In the Bridger Mountains, mule deer usually were restricted to 20 percent or less of the total area during winter and average deer densities were 2- to 12-fold (ave. 4.7-fold) higher than during summer (Pac *et al.* 1991). Under extreme midwinter conditions, densities on winter habitat along the west slope reached nearly 190 mule deer/km^2 (Mackie *et al.* 1976). Seasonal increases in density tended to be highest where winter maintenance habitats comprised smaller proportions of the total yearlong habitat used by deer. The greatest increase (11.7-fold, 1.4-16.7/km^2) occurred on the Battle Ridge unit where winter habitat comprised only 8.5 percent of the total unit area.

Spatial distributions of mule deer in timbered breaks and prairie-badlands environments followed the clumped or aggregated pattern typical of animals occupying patchy environments (Elseth and Baumgardner 1981). Areas of high density were either bordered by areas of declining density (Hamlin and Mackie 1989) or interspersed among low density and vacant areas (Wood *et al.* 1989). In the Missouri River Breaks, mule deer occurred on about 83 percent of the area yearlong, 64 percent during summer, 60 percent in autumn, 65 percent in winter, and 53 percent in spring (Hamlin and Mackie 1989). For Cherry Creek, averages were 37 percent overall, 20 percent in autumn, 19 percent in winter, and 15 percent in spring (Wood *et al.* 1989). However, because both areas experienced highly variable environmental conditions during all seasons, spatial distribution and deer densities were in a constant state of flux relative to availability of space, food, and cover.

Increases and decreases in population size in the Missouri River Breaks were marked by disproportionate changes in deer numbers in areas outside core habitats (Hamlin and Mackie 1989). While density increased or decreased across broad areas, densities in core areas changed little, if at all, because young females did not use the same sites as established matriarchs during summer and early autumn. Similar to the findings of Van Horne (1983), at high population levels, deer density in lower quality habitat could equal or exceed that in high quality core areas (Hamlin and Mackie 1989).

A similar relationship appeared to prevail among white-tailed deer on the lower Yellowstone River. Again, at low population levels all females were able to occupy optimal reproductive habitat. As deer numbers increased, young adult females increasingly occupied low quality habitats such that densities in optimal habitats did not increase until high population levels were attained (Dusek *et al.* 1989).

Sex and Age Composition

Within the context of our studies, sex and age composition refers to the relative abundance of adult males and females, young and adults in a population. Measurement may be in terms of either absolute or relative numbers (i.e., ratios or percentages).

The numbers or proportions of deer in different sex and age classes varied within and among populations and habitats. Some of the variation appeared to occur within a "normal range," for a particular environment (Tables 1 and 2). Because of this, sex and age composition may be indicative of basic deer-habitat relationships; that is, how well each habitat meets the specific requirements of each sex and age class of deer. However, variation in composition influenced by environmental fluctuation, hunting, sampling, and factor interaction often confounded analyses of factors determining sex/age composition within and among population units.

Table 1.
Post-hunting sex and age ratios for mule deer populations on three Montana study areas.

Areas/Years	Population	Males:100 Females	Fawns:100 Females
Bridger Mountains 1971-87	NW Slope	26 (8-40)[a]	51 (9-85)
1974-87	Bracket Creek	11 (5-15)	61 (33-91)
Missouri River Breaks 1960-87	–	31 (13-49)	65 (29-116)
Cherry Creek 1975-87	–	18 (7-36)	72 (48-111)

[a] average (range)

Table 2.
Post-hunting sex and age ratios for white-tailed deer populations on two Montana study areas.

Areas/Years	Males:100 Females	Fawns:100 Females
Cherry Cr. 1975-87	28 (17-47)[a]	74 (34-120)
Lower Yellowstone River 1980-87	25 (18-37)	83 (58-112)

[a] average (range)

Sex Composition

Among adults ≥1 year, females outnumbered males by up to 6:1 pre-hunting season and 20:1 post-hunting season. Some of these differences were influenced by selective hunting and variation in hunting pressure; others apparently were related to characteristics of the environment occupied by deer. We found no evidence that adult sex ratios attain equality in free-ranging deer populations even under differentially heavy harvest of antlerless animals. Females may outnumber males by 2:1 or 3:1 even in unhunted populations of mule deer (Martinka 1978) and white-tailed deer (Gavin *et al.* 1984, Kie and White 1985). Certain environments may provide opportunity for greater local occurrence of adult males relative to females while others may limit the occurrence of adult males. High proportions of maintenance habitat interspersed with reproductive habitat may be necessary for an area to support many adult males or exhibit a high sex ratio (Hamlin and Mackie 1989). On the lower Yellowstone River, adult males were more abundant during autumn on the vegetationally and agriculturally more diverse Elk Island (ave. = 53 males:100 females; range 26-73:100) as compared with the Intake subpopulation unit (ave. = 38:100, range 20-49:100).

Long-term trends in relative abundance of male and female mule deer in the Missouri River Breaks and Bridger Mountains show the relative influence of different hunting strategies on sex composition. The two populations were hunted under varying regulations designed to both limit and enhance hunting pressure and harvest of antlerless deer at different times. In the Breaks (Fig. 31), adult male:100 female ratios declined generally from the mid-1970s through the mid-1980s. During the 1960s and early 1970s, regulations emphasized increased hunting pressure and harvest of antlerless deer through 2-deer either-sex hunts, unlimited low-cost nonresidents licenses, and special early and late season hunts. At that time, as hunting pressure and harvests increased, the proportion of antlerless deer killed also increased from less than one-third to one-half or more of the total harvest (unpubl. MFWP harvest data). Post-season sex ratios averaging 40 adult males:100 females were recorded during 1960-74 (Hamlin and Mackie 1989).

The sharp decline in mule deer numbers in the Breaks during 1972-75 (Fig. 31) resulted in restriction of harvest to "bucks only" from 1976 through 1980. This shift in harvest strategies increased mortality of adult males relative to adult females.   As a result, as the population recovered, the adult female segment increased by 111 percent from

High proportions of maintenance habitat interspersed with reproductive habitat may be necessary for an area to support many adult males or exhibit a high sex ratio.

Figure 31.
Trend in numbers
of adult males and
females, male:100
female ratio, and
percent males in
the Missouri River
Breaks mule deer
population, early
winter 1960-61
through 1986-87.
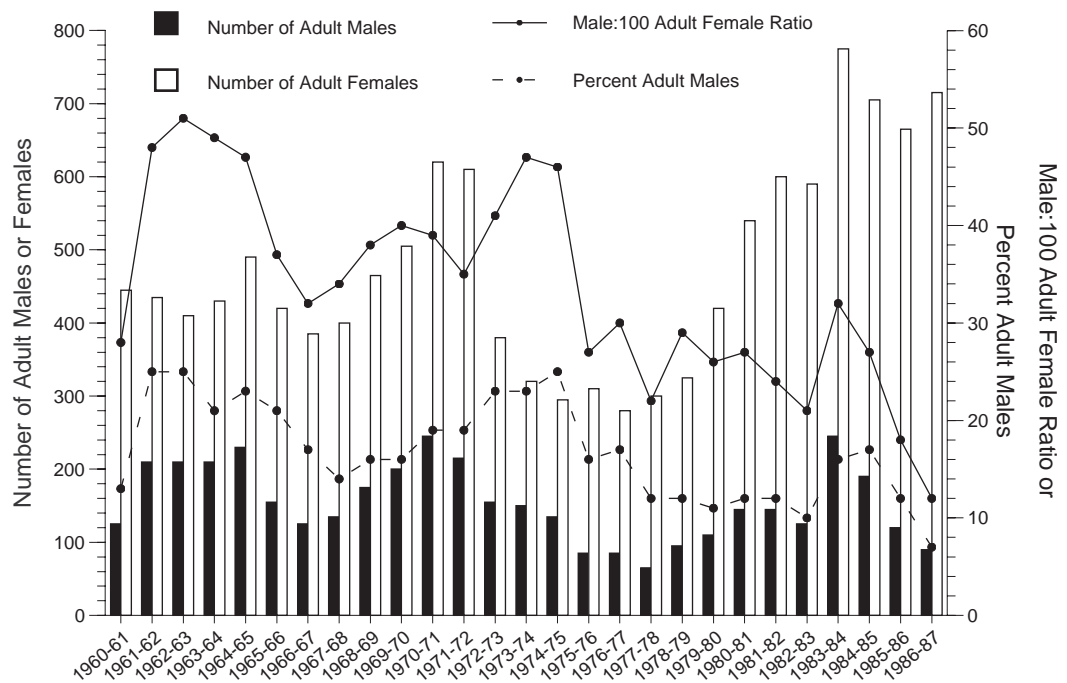
...in the Breaks population, sex ratio was influenced as much or more by numbers of females as by numbers of males.

1976 through 1982 while numbers of adult males increased only 47 percent (Hamlin and Mackie 1989). Although either-sex hunting resumed in 1981, hunter harvests of females did not reach rates equivalent to those of the 1960s. Numbers of adult females peaked during 1983-84 and fluctuated at relatively high levels through the late 1980s, while buck numbers decreased from 1983 through 1986. Perhaps as a result of hunter selection for mature bucks, the mean post-season adult sex ratio declined from 40 males:100 females during 1960-74 to less than 25:100 females during 1975-87. Bucks ≥ 2 1/2 years comprised an average of 31 percent of males classified in early winters 1960-80, compared with 20 percent during 1981-87.

Overall, in the Breaks population, sex ratio was influenced as much or more by numbers of females as by numbers of males. Numbers of females were high and gradually increasing through much of the period from 1977 to 1987; numbers of males were relatively low and stable, ranging from 100 to 200 post-season in most years. This resulted at least partially because of reduced harvest of females associated with changes in harvest regulations and reduced desire of hunters

to harvest antlerless deer. Thus, the low and decreasing ratios after the mid 1970s were more the result of increased numbers of adult females and factors influencing that increase than a reduction in absolute numbers of adult males in the population.

Also, increases in numbers of adult females reflected environmental conditions favorable to relatively high recruitment and adult survival during the late 1970s and early 1980s (Hamlin and Mackie 1989). For example, changes in livestock grazing, favorable weather conditions, and improved range condition beginning in the late 1970s may have increased the quantity and/or quality of reproductive and summer maintenance habitat that sustained progressively greater numbers of females on the area. Decreased hunter selection for and harvest of adult females during years of favorable environmental conditions and high recruitment could have led to increased numbers of young females settling in habitats that provided resources necessary for survival but not reproduction as described for deer populations in the prairie-badlands environment (Wood *et al.* 1989).

In the Bridger Mountains (Fig. 32), adult male:female ratios declined similarly to those in the Missouri River Breaks following onset of bucks-only hunting in the mid 1970s, then increased with population growth during the early 1980s and declined to 1987. A special regulation limiting harvest of older males during the last 2 weeks of the hunting season was implemented in 1989 (Pac and Ross 1993). Subsequent studies (Pac unpubl. data) indicate that numbers and proportions of bucks increased again from 1987 to the early 1990s before declining. However, increases in buck numbers through the early 1990s were related primarily to above-average recruitment rather than any long-term reduction in hunting mortality.

In contrast to the Missouri River Breaks, numbers of females in the Bridger Mountains were relatively stable throughout the period of study, and sex ratios appeared to be influenced more by trends in the number of adult males in the population. Also, harvest of females has always been light, at least since the mid 1970s. The light harvests of females apparently contributed to maintenance of stable female numbers while selective harvest of adult males

more closely tracked their abundance in the population.

Numbers of adult males and male:female ratios for the South 16-Mile population increased considerably after hunting was greatly restricted on private lands that comprise much of that area. Most of the increase seemingly resulted from increased survival of mature males (Fig. 33). In contrast, total adult male:female and 4-point-male:female ratios for heavily hunted populations occupying public land showed little improvement or declined through the period (Pac unpubl. data).

Data sets that track variation and trends in sex ratios (numbers of males:100 females) were limited for mule deer in other study areas and for white-tailed deer generally. Buck:doe ratios were affected by recruitment and harvest strategies in all areas. As hunting pressure, numbers of antlerless permits, and harvest rates changed, buck:doe ratios also changed.

On the Cherry Creek study area, numbers of female mule deer increased about 6-fold from 1975-76 through 1983-84 before declining. Post-season male:female ratios varied, but were
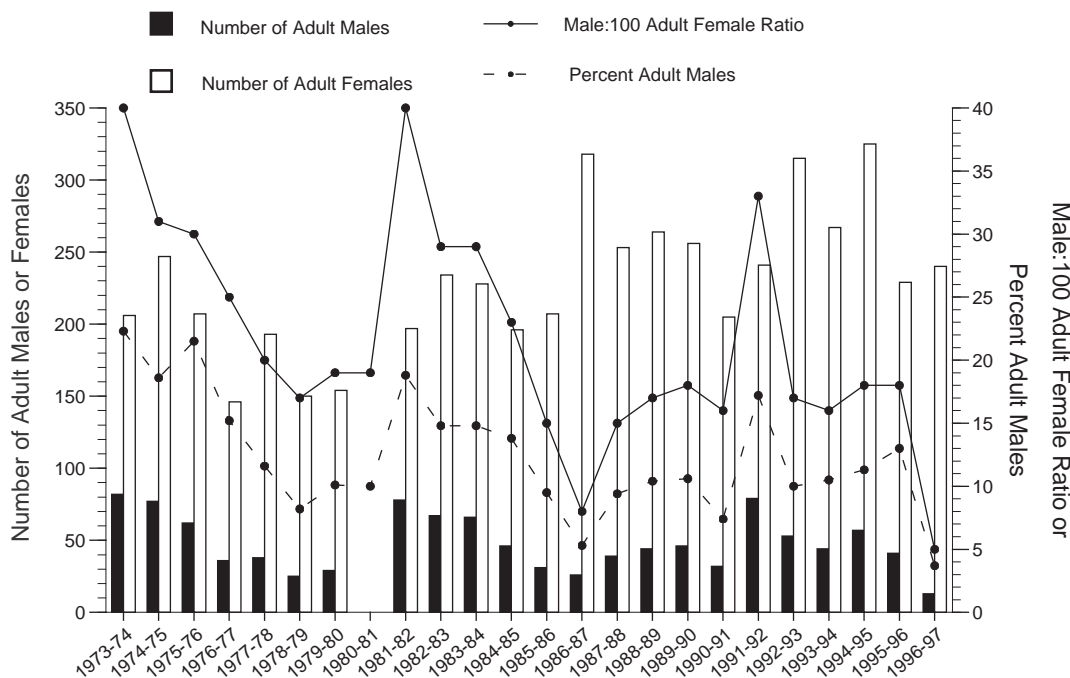
Figure 32. Trends in numbers of adult males and females, male:100 female ratios, and percent males in a mule deer population on the northwest slope of the Bridger Mountains, early winter 1973-74 through 1996-97.
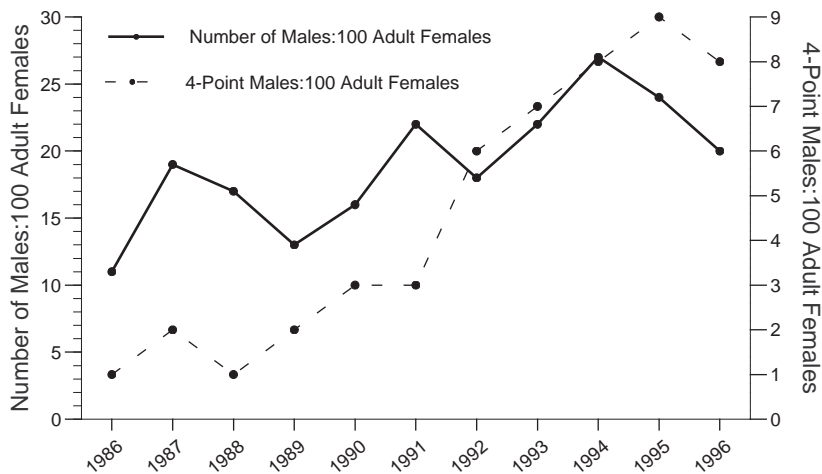
Figure 33.
Relative trends in post-hunting male:100 female and 4-point-
male:100 female ratios for the South 16-Mile mule deer
population, Bridger Mountains, 1986-96.

relatively high in 1976 and 1977 as deer numbers began increasing and declined to 10-20 males:100 females during 1978-1985 (Wood *et al.* 1989). As a result, sex ratios varied inversely with numbers of adult females in the population. For the smaller whitetail population, numbers of adult males and adult females, as well as sex ratios tracked one another from 1975-76 through 1983-84. Thereafter, heavy selective hunting of females under multiple antlerless permits led to disproportionately higher mortality of females such that post-season male:female ratios increased while numbers of both sexes declined.

On the lower Yellowstone River, white-tailed deer numbers increased with increased numbers of adult females from 1980-81 to 1983-84 and declined slightly to 1985-86. Numbers of males remained relatively stable throughout the study, while post-hunting sex ratios inversely tracked adult female numbers.

Although sex ratios and/or the percentage of males are commonly taken as measures of the abundance of adult males, we found highly variable relationships between numbers of adult males and females, male:female ratios, and percent males in the populations we studied. In the Missouri River Breaks and Bridger Mountains relatively high sex

ratios and percentages of males occurred during periods when total population size was high (Figs. 31 and 32), but the converse was also true. However, sex ratios and percent bucks could decrease because of increased numbers of adult females. Differences in percentages of bucks also reflected the influence of variation in numbers of young in the population.

Use and interpretation of ratios as indices of population status or for management prescription requires knowledge of actual numbers of adult males and females in a population. Ratios do not reflect the total numbers of bucks available to hunters, only the relative proportions of bucks and does that hunters might observe in the field. Where numbers were available, ratios were less important. However, ratios indicate relative observability of bucks versus antlerless deer, and if ratios are low, many hunters may perceive few bucks even when numbers are high.

Age Composition

Both percent fawns and fawn:100 adult ratios generally tracked fawn numbers and trends in populations during most years, though some discrepancies occurred. The two parameters reflected variation in numbers of adults as well as fawns. Over time, similar percentages and ratios were associated with large differences in numbers of fawns and/or adults in a population (Figs. 34, 35, and 36). Often, especially in prairie deer populations, fawn percentages were highest and ratios peaked 1-4 years prior to peaks in total numbers of fawns and total deer in a population. Maximum fawn recruitment to spring did not exceed 40-45 percent of total mule deer and 45-50 percent of whitetail populations on any of the areas studied, suggesting this may be a "biological cap" for these species in Montana ecosystems. Comparison of trends in spring fawn:100 adult ratios for mule deer among populations and habitats (Fig. 37) shows that each population exhibited trends characteristic
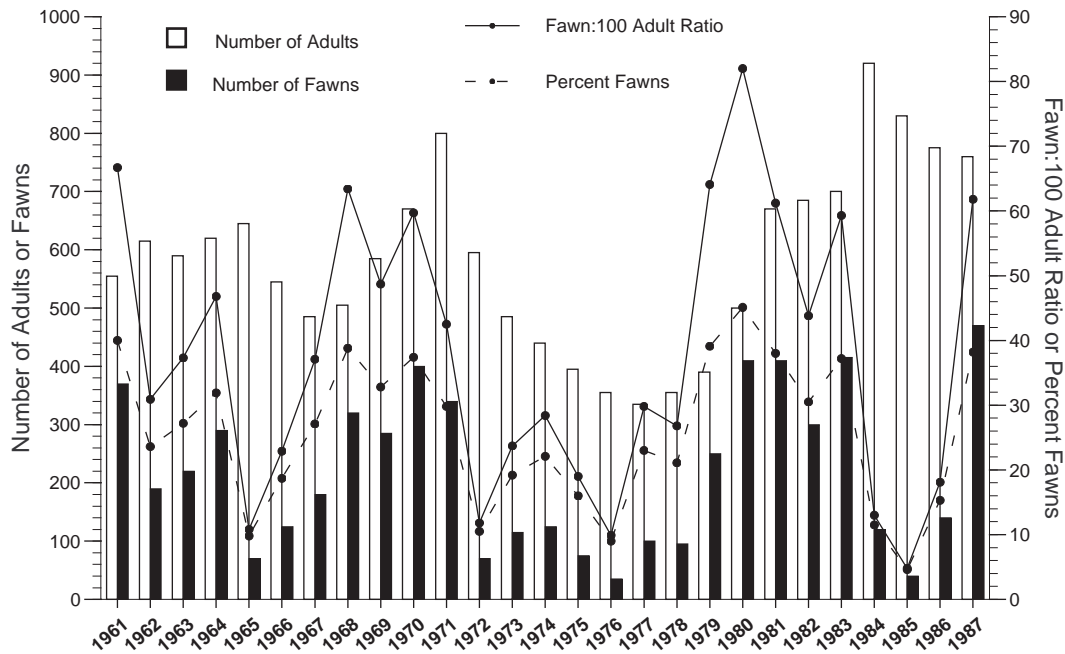
Figure 34.
Trends in estimated total numbers of adults and fawns, fawn:100 adult ratios, and percent fawns in the mule deer population on the Missouri River Breaks study area, spring 1961-1987.

Use and interpretation of ratios as indices of population status or for management prescription requires knowledge of actual numbers of adult males and females in a population.
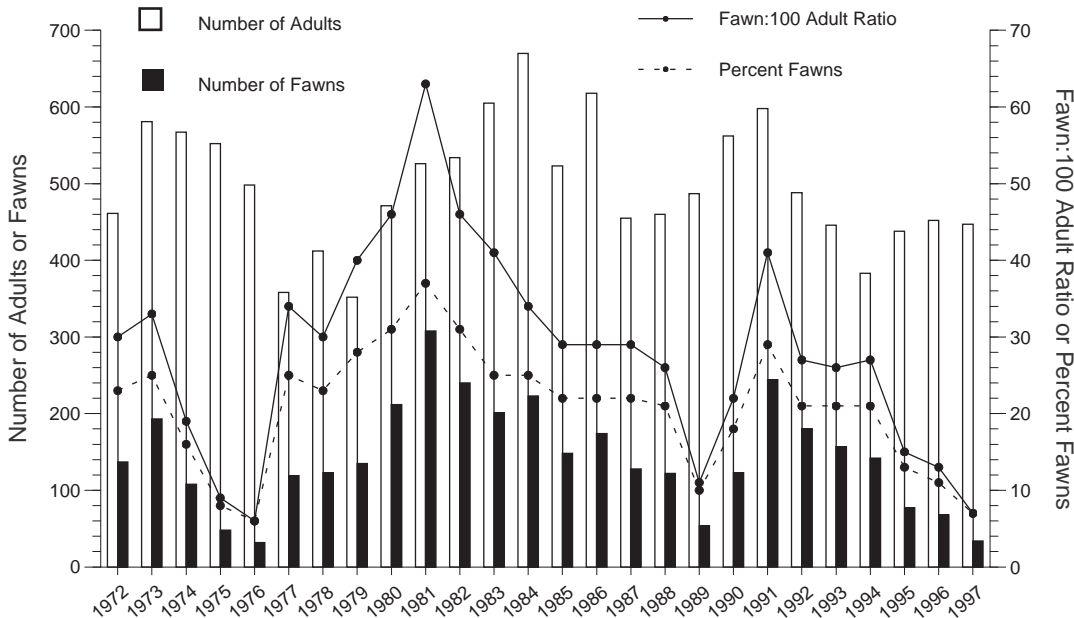
Figure 35.
Trends in estimated total numbers of adults and fawns, fawn:100 adult ratio, and percent fawns in the mule deer population on the Northwest Slope, Bridger Mountains, spring 1972-1997.
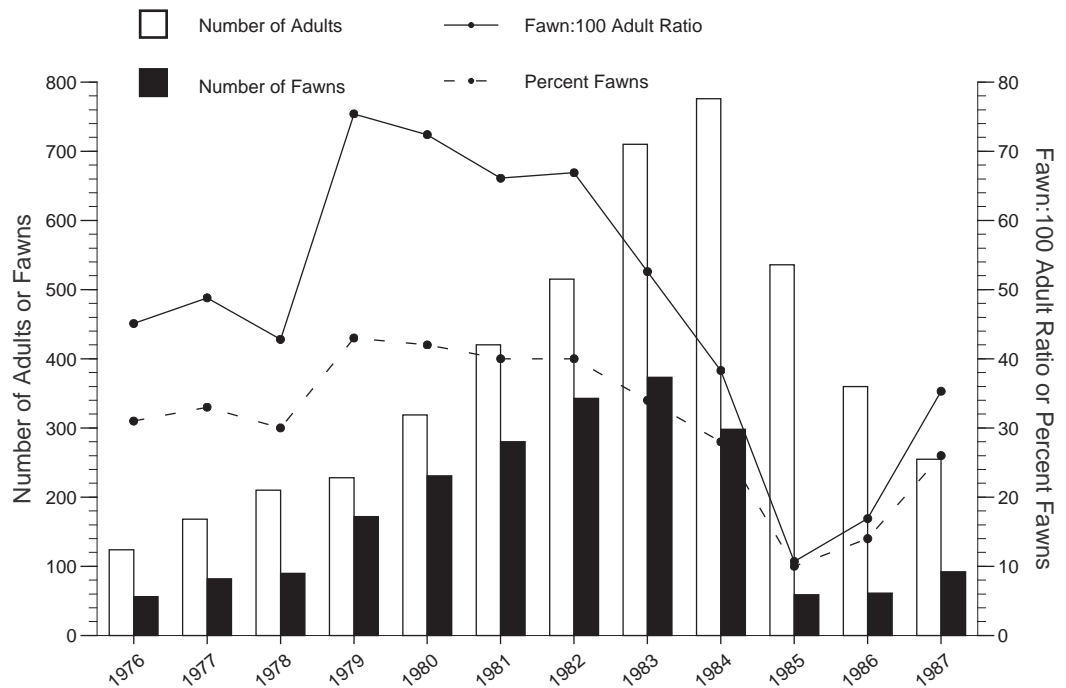
Figure 36.
Trends in estimated total numbers of adults and fawns, fawn:100 adult ratios, and percent fawns in the mule deer population on the Cherry Creek study area, spring 1976-1987.
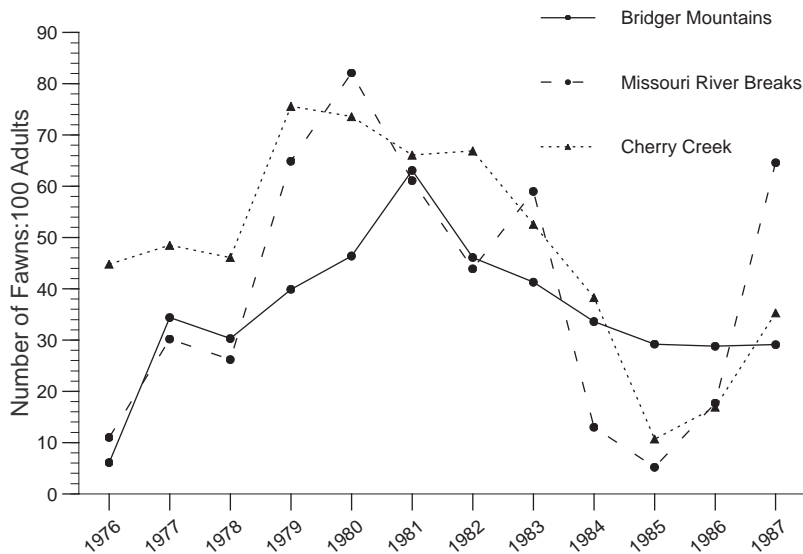
Figure 37.
Comparison of trends in number of fawns:100 adults on Bridger Mountain, Missouri River Breaks, and Cherry Creek study areas during spring 1976-1987.

of the environment in which it occurred. Generalizations across populations and habitats based on "biological potential" rarely applied. Because of this and the failure of ratios and percentages to consistently track numerical changes, interpretation of population trends and management opportunity from age composition data alone could be misleading. At least some knowledge or estimate of numbers of adult females or adults at the time is required.

Age Structure

Age structure is the number or proportion of deer in successive age classes from young of year through the oldest surviving animals. It represents a combination of annual production/recruitment of young, emigration/immigration of yearlings or young adults, and adult survival between age classes. Thus, age structure reflects the cumulative effect of all factors influencing past gains and losses to a population.

Age structure is most useful for determining what has happened to a population in the past (Hamlin and Mackie 1989) and may be misleading in predicting population status and trend. Like other sex and age compositional parameters, age structure data are best applied in conjunction with some measurement or estimate of population size and trend.

Generalizations about age structure and relative survival rates by sex and age class based on age structural data alone (i.e., construction of life tables) should be viewed with caution. Data for mule deer across a spectrum of habitats and for different populations within the Bridger Mountains indicated that "stable" age structures probably cannot be expected for this species. Persistence of a stable age structure requires constant natality and mortality. On our study areas, natality and mortality occurred in periods of both "boom" and "bust years" resulting in shifting age structures. There was no "typical" age structure for the species across habitats, between populations, or over time for any one population.

We identified four different types of age structure that occurred during some years within the female and male segments of mule deer populations (Fig. 38):

- Type 1 - a pyramidal age structure, heavily skewed to young age classes, considered characteristic of populations experiencing rapid increase as a result of high recruitment of young and/or relatively low annual adult survival (i.e., high annual turnover);

- Type 2 - a relatively flat or low pyramid age structure, resulting from periods of low and stable recruitment and high longevity among adults (i.e., low annual turnover);

There was no "typical" age structure for the species across habitats, between populations, or over time for any one population.
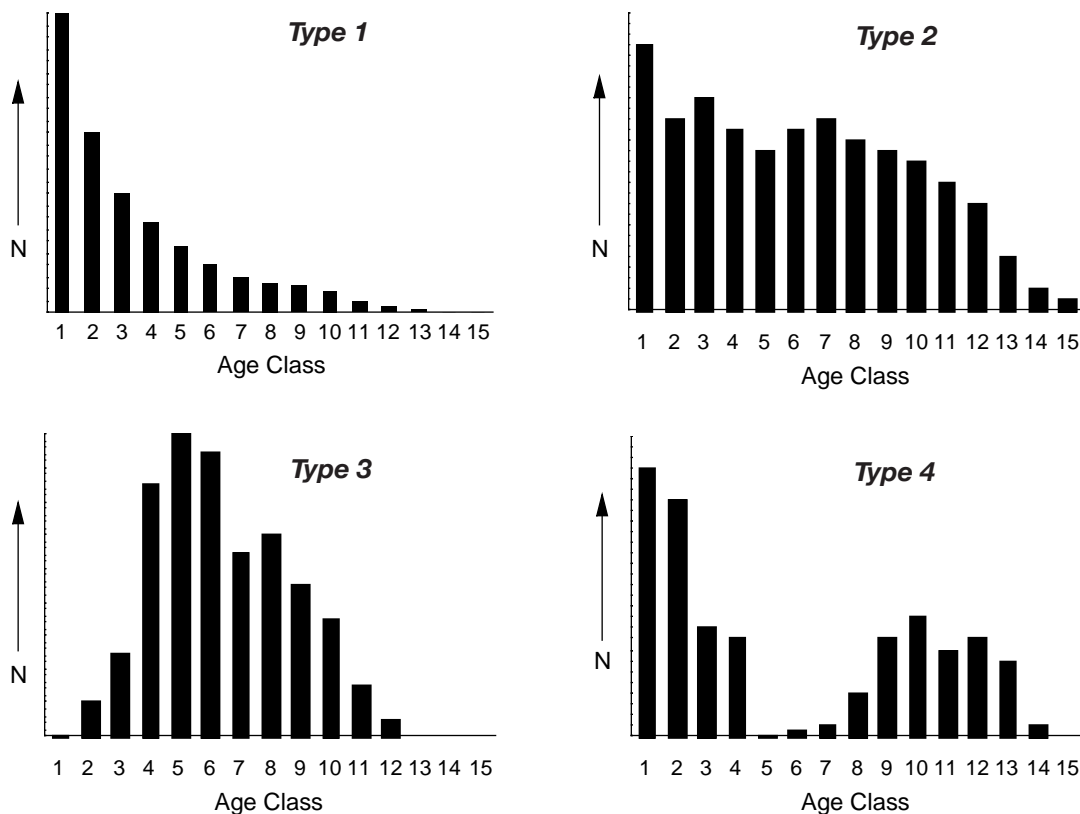
Figure 38.
Conceptualized examples of four types of age structures observed in Montana mule deer: Type 1 = pyramidal, Type 2 = flat or low pyramid, Type 3 = convex, Type 4 = concave or "U" shaped.

- Type 3 - a convex age structure, dominated by middle or "prime" age classes and associated with sharply reduced or declining populations (Elseth and Baumgardner 1981) and;
- Type 4 - a concave or "U"-shaped age structure containing more individuals in young and old age classes than in middle age classes and associated with population recovery following a decline (Pac *et al.* 1991).

Populations in specific habitats may have spent more time in either type 1 or type 2 age structures, thereby implying characteristic age structures by habitat. However, both type 1 and 2 structures occasionally occurred in any population in response to various environmental stimuli. Type 3 age structure occurred only temporarily in delayed association with severe environmental events and conditions resulting from low recruitment in youngest cohorts for 1 or more years combined with high mortality in old age classes. High natural survival rate among residual, prime-aged deer sometimes maintained this age structure to some degree for several years until increased recruitment began to skew the age distribution toward the Type 4 age structure, which was also temporary.

At any given time, individual populations could exhibit very different age structures resulting from environmentally-induced variation and hunting. For example, during two years when comparable data were obtained, age structures of female segments of four different populations in the Bridger Mountains varied from strongly pyramidal to somewhat "U"-shaped (Fig. 39). Male age structure was essentially pyramidal in all populations; apparently because hunters heavily selected for older, large antlered males. Because of lower total numbers of males, even low annual recruitment provided sufficient numbers of male fawns and yearlings to maintain the pyramidal structure during most years under all but the most severe environmental conditions.

Age structural dynamics and trends for mule deer females (Fig. 40) and males (Fig. 41) through periods of population decline and recovery in the Bridger Mountains and Missouri River Breaks further illustrate the mix and succession of age structures that occur over time. Prior to decline, female age structure on the northwest slope of the Bridger Mountains included representation of young, middle-age, and older deer. Losses of three successive cohorts and substantial numbers of old females through the decline resulted in a strongly convex, Type 3 age structure 3 years later. Thereafter, high survival of residual prime-age adult females combined with low but stable recruitment maintained the female segment for several years until increased recruitment provided opportunity for gradual population increase during the early 1980s. Cohorts were never sufficiently large, nor adult survival so low as to shift female age structure toward the pyramidal Type 1.

The age structure of male mule deer in the Bridgers exhibited a somewhat different trend. Numbers of males were reduced through the 1974-75 winter resulting in an age structure dominated by prime-age bucks during 1975-76. Harvests and low recruitment further reduced buck numbers to a few individuals of various ages by winter-spring 1978. The increased cohort size in 1980 was sufficient to shift male age structure to the pyramidal form by 1981-82 (Fig. 41).

Age structure of mule deer in the Missouri River Breaks, measured and estimated through population modeling for spring 1968-86 (Hamlin and Mackie 1989), was highly variable and shifted through two different periods of population increase, 1968-71 and 1979-83 and two periods of decline, 1972-74 and 1984-86. Age structures changed similarly through both periods of population increase and decline, though the mid 1970s decline was more severe and resulted in a lower population.

All basic age structural types were represented through the major population fluctuation in the 1970s. For example, by 1970-71, following 4-5 years of
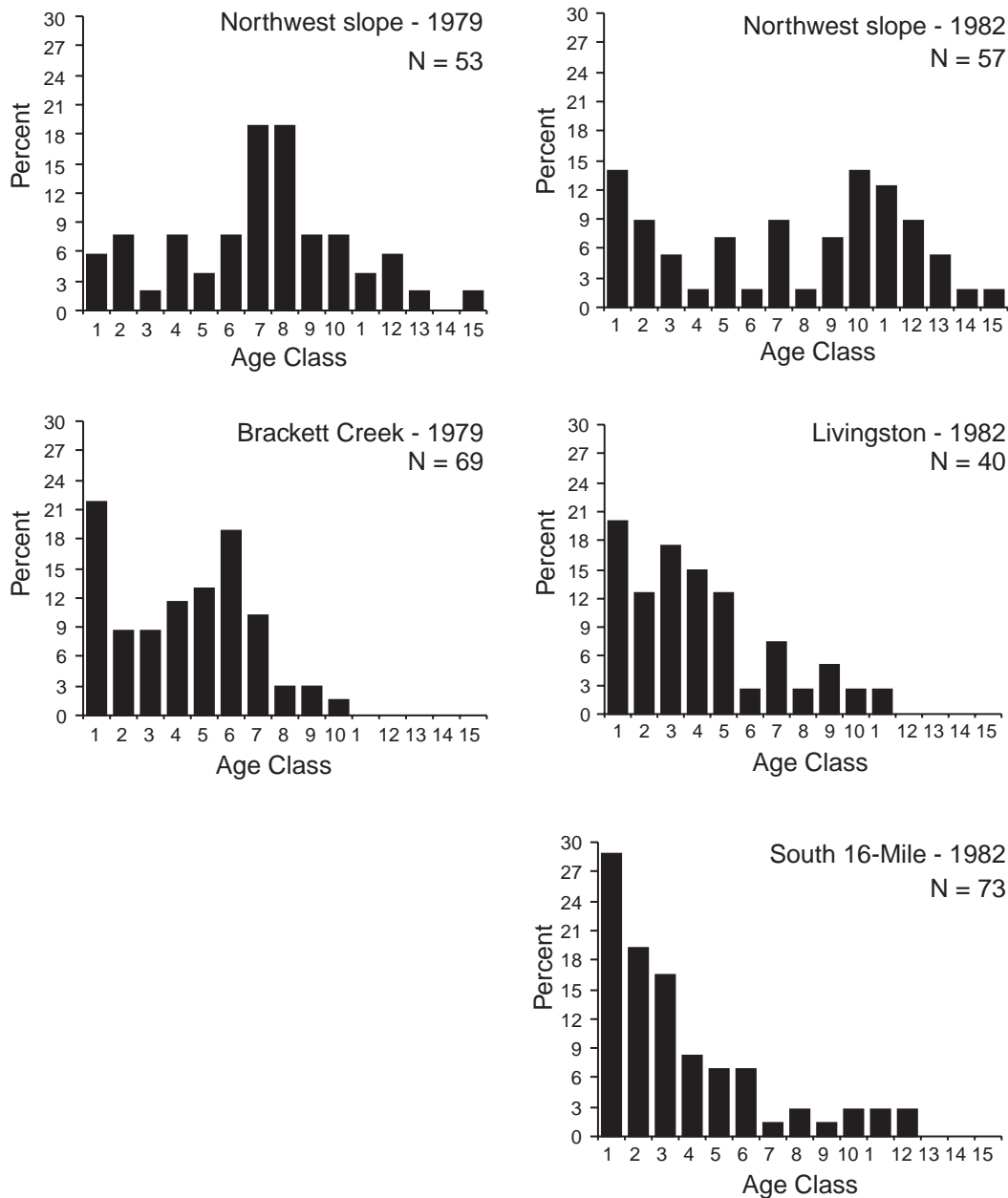
Figure 39.
Comparative age structures for adult females in four mule deer population-habitat units in the Bridger Mountains illustrating the mix of different age structures possible in adjacent populations during a given year (after Pac et al. *1991).*

At any given time, individual populations could exhibit very diffrent age structures resulting from environmentally-induced variation and hunting.

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population increase, both female and male segments exhibited distinct pyramidal age structures. High winter mortality of fawns and older adults during 1971-72 abruptly shifted age distributions to Type 3; few deer of either sex remained that were less than 2 or older than 6 years of age. Small annual cohorts and light to moderate adult mortality further reduced deer numbers by 1974-75, when low recruitment combined with high survival of adults to older age classes resulted in small populations with relatively flat, Type 2 age structures through spring 1978. Increased annual cohorts fostered rapid population growth and shifted age distributions back toward pyramidal (Type 1), for the smaller male segment during 1979-83 and for females during 1980-83.

Northwest Slope Bridger Mountains

Missouri River Breaks
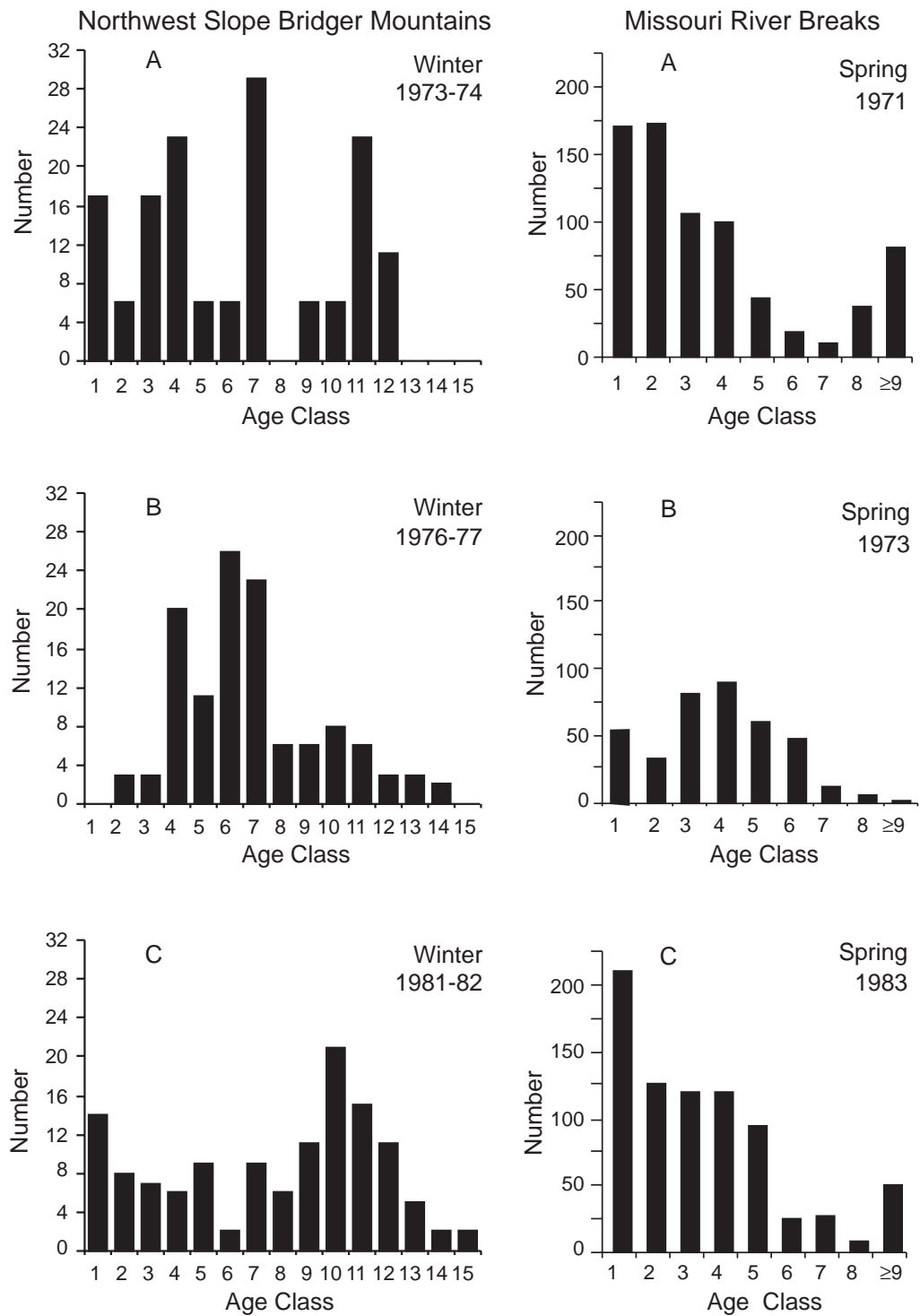
Figure 40.
Age structural dynamics of adult female mule deer in the Bridger Mountains and Missouri River Breaks. A = prior to severe winter, B = one full year following severe winter, C = following several years of population growth (after Pac et al. 1991 and Hamlin and Mackie 1989).

Northwest Slope-Bridger Mountains   Missouri River Breaks
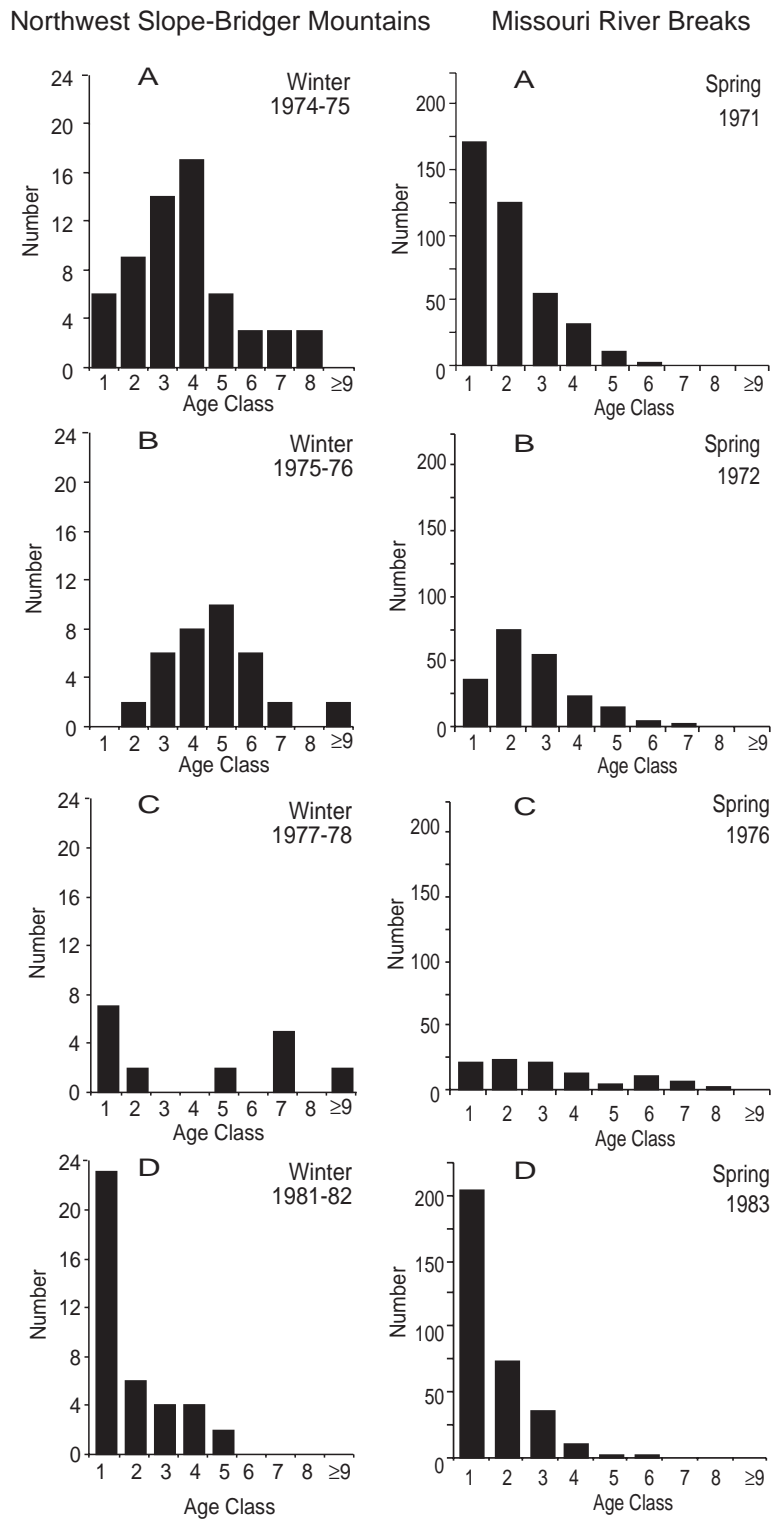
Figure 41.
 Age structural dynamics of adult male mule deer in the Bridger Mountains and Missouri River Breaks: A = during or prior to severe winter, B = year following severe winter, C = at population low, and D = following several years of population growth or recovery (after Pac et al. *1991 and Hamlin and Mackie 1989).*

Recurrent low recruitment and small cohorts in the Breaks during 1984 and 1985 shifted age distributions for both sexes sharply toward the type 3 again during 1984-86. Adult mortality remained low and the female population did not decline, but more or less continued to increase following the trend established in 1977-78. With continued hunter harvests, numbers of adult males declined as in the mid 1970s when a similar age structure prevailed.

Age structures for white-tailed deer inhabiting conifer forest habitat in the Swan Valley and riparian-agricultural habitat along the lower Yellowstone River were pyramidal and similar (Fig. 42). Younger age classes were better represented in the productive riparian-agricultural habitat where an average of 75 percent of autumn populations during 1980-85 was 2 years-old or less (Dusek *et al.* 1989) compared with 60 percent in the Swan (MFWP unpubl data). Individuals 8 years and younger comprised more than 90 percent of all does on both areas, while few males lived longer than 4 years.

Age structures for the Swan and lower Yellowstone River were for populations at or near peaks following several years of increase. Comparative

Figure 42. Comparison of representative adult male and adult female age structures for white-tailed deer on the Swan Valley and Lower Yellowstone River study areas (MFWP unpub., Dusek and Mackie 1988).
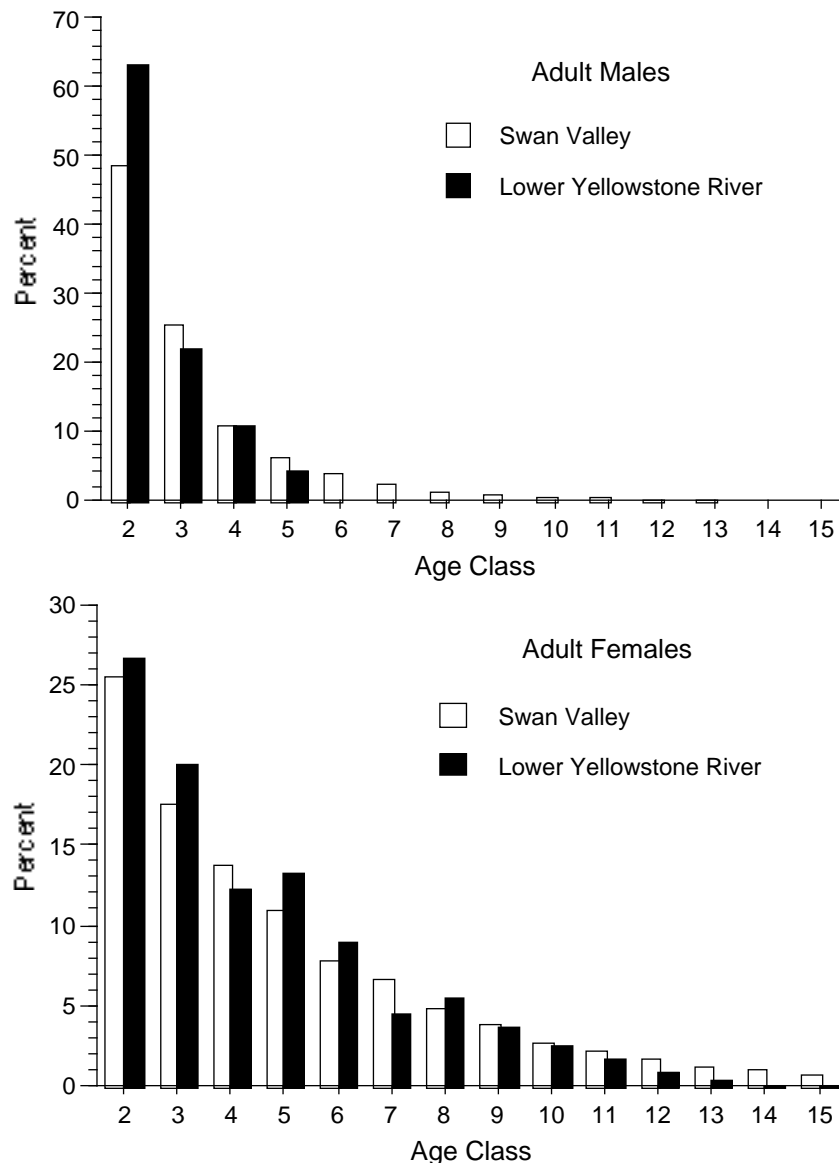
age structures for the lower Yellowstone River during 1980-85 (Fig. 43) (Dusek *et al.* 1989) and age structure of white-tailed deer examined at hunter checking stations in the Swan Valley during 1974-1989 (Coates 1996) indicate that age structures were more stable than those recorded for mule deer. This probably occurred because of the more stable environments occupied by these white-tailed deer. Large fluctuations in age composition of whitetails on the Cherry Creek study area reflected boom and bust natality and mortality similar to mule deer in plains environments.

In populations of both species, adult females greatly outnumber adult males in winter and spring. Because of this, the size of each annual cohort has a proportionately greater effect on total numbers and age distribution of males than females. Differential heavy harvests of males also reduces the influence of strong year classes of young sooner in the male segment. Combined with hunter selection for the largest available antlered males, this results in male age structures retaining a more pyramidal shape across a wider range of habitats and population size than for females.
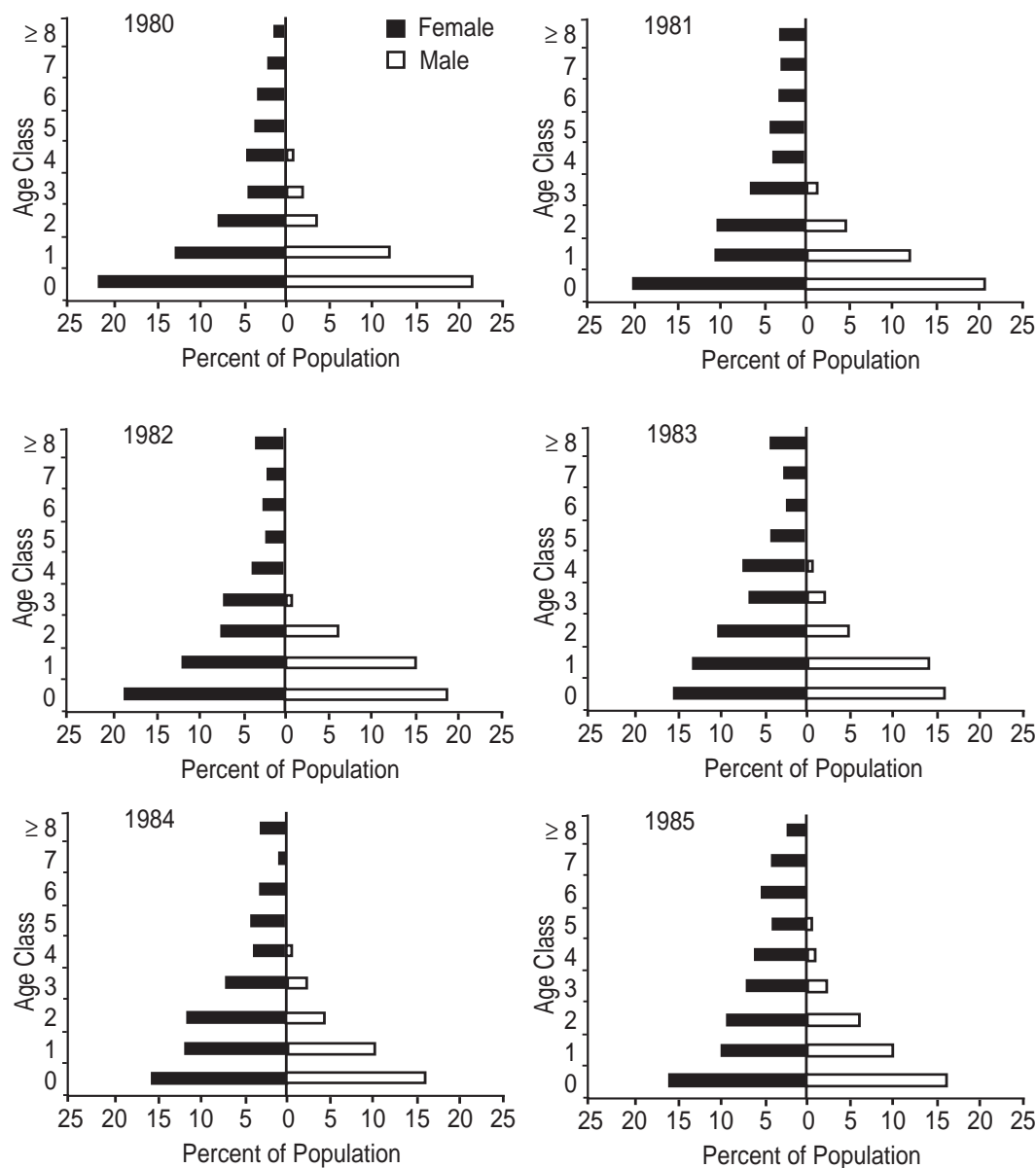
Figure 43. Age structure of female and male white-tailed deer on the lower Yellowstone River during autumn 1980-85 (Dusek et al. *1989).*

Population Dynamics

...factors affecting mortality rates of fawns generally have greater impact on recruitment than those affecting initial production.

Understanding population dynamics requires knowledge of factors influencing fawn recruitment and adult mortality and how they interact to change deer numbers over time. We use recruitment to mean reproductive potential less all fawn mortality through the year following birth.

The influence of fawn mortality differs from adult mortality; factors affecting fawn mortality determine annual recruitment, whereas those affecting adult mortality determine population losses. Also, different factors may operate at different intensities on fawn and adult mortality. Immigration and emigration are special cases of recruitment and mortality and are difficult to quantify.

Reproduction and Recruitment

Reproductive rate (i.e. the number of fawns produced per doe at birth) varies among populations of both species (Cheatum and Severinghaus 1950, Robinette and Gashwiler 1950, Robinette *et al.* 1955, 1977). It also varies over time within populations. Although reproductive potential can vary, post-partum mortality is usually more variable. Thus, factors affecting mortality rates of fawns generally have greater impact on recruitment than those affecting initial production.

Fawns per productive female for mule deer in the Missouri River Breaks varied among years from 1.25 to 1.76 fawns:doe, with a mean of 1.58 fawns:doe, during 1975-1986 (Hamlin and Mackie 1989). Studies in other eastern Montana environments have indicated potential reproductive rates ranging from 1.52 (Jackson 1990) to 1.67/1.68 (Dusek 1971, Fritzen 1995) and 1.90 fetuses per mule deer female (Eustace 1971). Data from collections of reproductive tracts in the Bridger Mountains indicated lower potential reproduction for mule deer in that mountain-foothill environment (1.27 fetuses:female > 1 year of age) than for other Montana habitats (Pac *et al.* 1991).

Like other studies that have shown wide spatial and temporal variation in productivity of both mule deer and white-tailed deer (Beasom and Wiggers 1984), we found no consistent differences

in reproductive potential between the two species in Montana. Collections of white-tailed deer reproductive tracts in the Swan Valley (Mundinger 1981) and along the lower Yellowstone River (Dusek *et al.* 1989) revealed fetal rates averaging 1.50 and 1.68 fetuses:female, respectively. Smaller samples from other study areas suggested even higher rates, up to 2.0 fetuses:female on Missouri River bottomlands (Allen 1965) and 1.75 fetuses:female in the Salish Mountains (Morgan 1993). Within this framework, spatial variation in reproductive potential that occurred appeared related more to environment and population-habitat relationships than to species. Thus, whitetail females in the conifer forested Swan Valley exhibited lower reproductive potential than both their counterparts in riparian-agricultural habitat on the lower Yellowstone River (Fig. 44) and mule deer in some eastern Montana habitats. Subpopulations associated with different habitat complexes along the Yellowstone River also exhibited different reproductive potentials (Table 3).

Both in-utero and observed age-specific reproduction among marked deer indicate significant difference in productivity of females by age class. Fawns of both species rarely conceive and do not contribute to reproduction in Montana. This may reflect inability of fawns to achieve the size and physiological state necessary for sexual maturity or the combined effects of photoperiod and early winter weather in northern latitudes (Dusek et al. 1989). Among adult females, potential productivity typically was lowest and most variable in 2-year-old females, increased progressively to a maximum among 3-6-year olds, and then declined somewhat with age. Age-specific reproduction varied like other parameters, among populations and habitats (Figs. 44-46, Table 3).

Initial fawn production among mule deer in the Missouri River Breaks increased steadily with age to a peak among 6-year-old females, declined sharply at age 7, then stabilized at a level similar to 3-year olds (Fig. 45). Rates

of fawn rearing to 6 months paralleled initial production; 4- and 5-year old females were most successful in recruiting fawns to 12 months.

Table 3.
Variation in potential productivity and fawn survival to autumn between two subpopulations of white-tailed deer on the lower Yellowstone River, 1980-85 (after Dusek et al. *1989).*

Age (yrs)	Above Intake		Below Intake	
	n	% or ratio	*n*	% or ratio
Pregnancy rates				
Yearling	12	83%	23	91%
≥ 2	45	91%	52	98%
Fetal rates				
Yearling	7	100:100	11	155:100
≥ 2	16	156:100	26	200:100
Fawn-rearing success				
2	14	43%	27	78%
3	16	44%	25	92%
4-7	39	79%	51	90%
≥ 8	9	22%	12	92%
Survival to autumn (fawns:females)				
2	14	50:100	27	104:100
3	16	63:100	25	144:100
4-7	39	108:100	51	149:100
≥ 8	9	22:100	12	133:100
Percent multiple births				
2	6	17%	21	33%
3	7	43%	23	56%
4-7	31	35%	46	67%
≥ 8			11	45%

...spatial variation in reproductive potential that occurred appeared related more to environment and population-habitat relationships than to species.
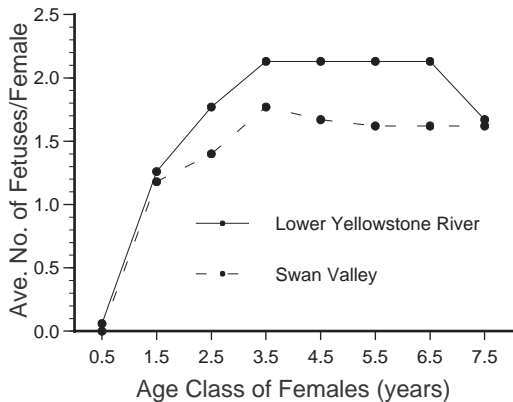
Figure 44.
Age specific in-utero fetal rates for white-tailed deer on the Lower Yellowstone River and Swan Valley study areas.
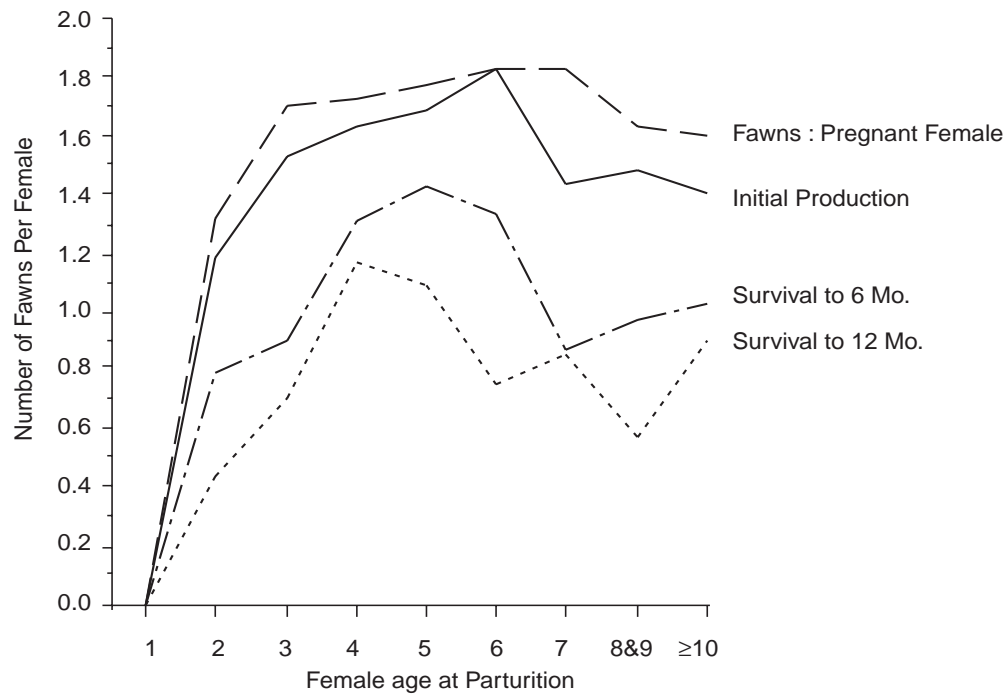
Figure 45.
Age-specific production and recruitment of fawns by female mule deer in the Missouri River Breaks, Montana, 1976-1984 (after Hamlin and Mackie 1989, 1991).
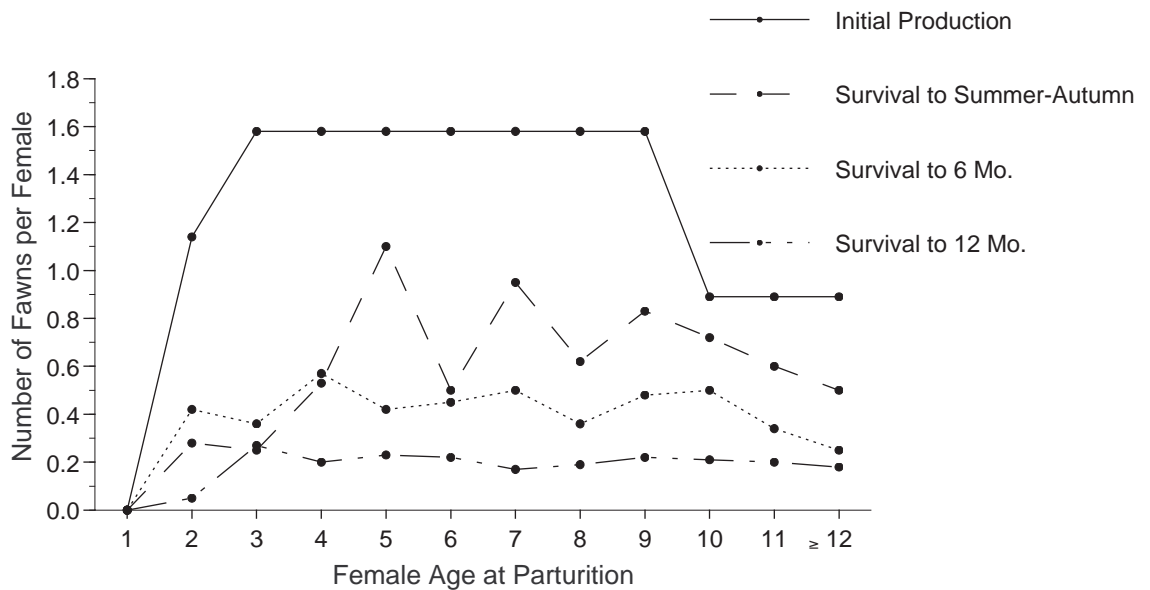
Figure 46.
Age specific production and recruitment of fawns by female mule deer on the west slope of the Bridger Mountains (after Pac et al. 1991).

In west slope populations in the Bridger Mountains, survival to summer-autumn increased progressively to a peak among 5-year-old females and then declined in a fluctuating pattern (Fig. 46). Females age 12 and older continued to rear fawns at a higher rate than 2- and 3-year olds and a similar rate to 4-year olds. Survival of fawns to winter declined in all but the youngest age classes of does; recruitment

in spring declined even further and became similar for females of all age classes 3 through 12 and older.

Survival of white-tailed deer fawns to autumn on the lower Yellowstone River increased with female age to 4 years, declined slightly to age 5, and increased again to a peak among 6-7-year olds before declining among females 8 years and older to about the same level as 2-year olds (Fig. 47). Age specific rates of fawn survival to autumn also differed between subpopulations (Dusek *et al.* 1989). Although all females reared fewer fawns on river bottoms above Intake as compared to the area below, fawn survival was especially low among youngest and oldest age classes above Intake (Table 3).

Survival of whitetail fawns to autumn and winter in the Swan Valley (Fig. 47) showed the same general increase with age as observed for deer elsewhere.

Some variation in annual reproduction appeared to occur among mule deer females ≥8 years of age in the Missouri River Breaks (Hamlin and Mackie 1989) and among young and old females in the Bridger Mountains (Pac *et al.* 1991). Irregular reproduction may also have been characteristic of youngest and oldest reproducing female white-tailed deer in the Swan Valley (Mundinger 1981). Reproductive patterns among marked deer indicated that females in the Missouri River Breaks and other variable, unpredictable environments may experience physiological exhaustion leading to both declining productivity and increased mortality in their fifth reproductive year, especially after periods when reproductive success has been high for several years (Hamlin and Mackie 1991).

Fawn recruitment rates varied across the spectrum of environments we studied (Table 4). Recruitment rates for mule deer were lower and more variable than for white-tailed deer. Based on both observed fawn:100 adult and modeled fawn:100 female ratios for mule deer, recruitment was lowest in the Bridger Mountains, followed by the Missouri River Breaks, and Cherry Creek prairie-

badlands habitats. The difference reflected variation in initial production and winter mortality of fawns among environments. Mean recruitment for white-tailed deer was similar among areas (Table 4) but was most variable on prairie-agricultural habitat along Cherry Creek.

Fawn Mortality

Average annual fawn losses up to three-fourths or more of potential reproduction were common in populations we studied. Mortality of fawns was high during early summer, dropped progressively through late summer and autumn to early winter, and then increased to mid-late winter (Fig. 48). About two-thirds of the total fawn mortality in mule deer populations occurred in summer and one-fourth during winter, but specific seasonal mortality patterns and rates varied widely among years. Two-thirds or more of annual mortality in fawn white-tailed deer also occurred in summer; winter mortality of fawns was light and averaged about 10 percent and 3 percent on the lower Yellowstone River and Cherry Creek areas, respectively.

Annual fawn mortality rates for individual populations ranged from a low average 32 (10-48) percent for white-tailed deer on the lower Yellowstone

Recruitment rates for mule deer were lower and more variable than for white-tailed deer.
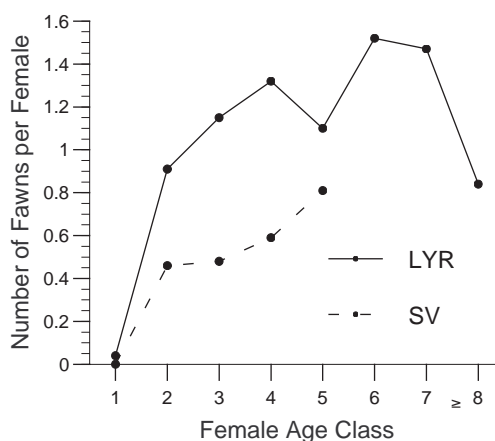
Figure 47.
White-tailed deer fawn survival by female age class to autumn on the lower Yellowstone River and early winter in the Swan Valley.

Table 4.
Mule deer and white-tailed deer fawn recruitment in Montana.
Data are observed fawn:adult and modeled fawn:female ratios in
spring (ave. ±1 SD).

Environment Study area	Observed Fawn:100 Adult Female Ratio	Modeled Fawn:100 Ratio[a]
MULE DEER		

Mountain-Foothill
  Bridger Mountains
  (Northwest Slope)
	29 ± 13
	range 6-63
	CV[b] = 0.45
	N = 25 years
		33 ± 13
		range 4-53
		CV = 0.39
		N = 14 years

Timbered Breaks Missouri River Breaks	40 ± 23 range 5-82 CV = 0.58 N = 21 years	51 ± 27 range 6-103 CV = 0.53 N = 28 years
Prairie-Badlands Cherry Creek	48 ± 21 range 11-76 CV = 0.44 N = 12 years	56 ± 24 range 13-90 CV = 0.43 N = 12 years
WHITE-TAILED DEER		
Northwest Montane Forest Salish Mountains	54 ± 13 range 26-71 CV = 0.23 N = 11 cases, 7 years	67 ± 18 range 30-96 CV = 0.27 N = 11 cases, 7 years
Riverbottom Agricultural Lower Yellowstone	58 ± 18 range 37-81 CV = 0.31 N = 6 years	75 ± 20 range 52-101 CV = 0.27 N = 6 years
Prairie-Agricultural Cherry Creek	53 ± 27 range 17-92 CV = 0.51 N = 11 years	66 ± 30 range 24-110 CV = 0.45 N = 11 years

[a] Assumes buck:doe ratio same as early winter.

[b] CV = coefficient of variation (CV = s/ x)
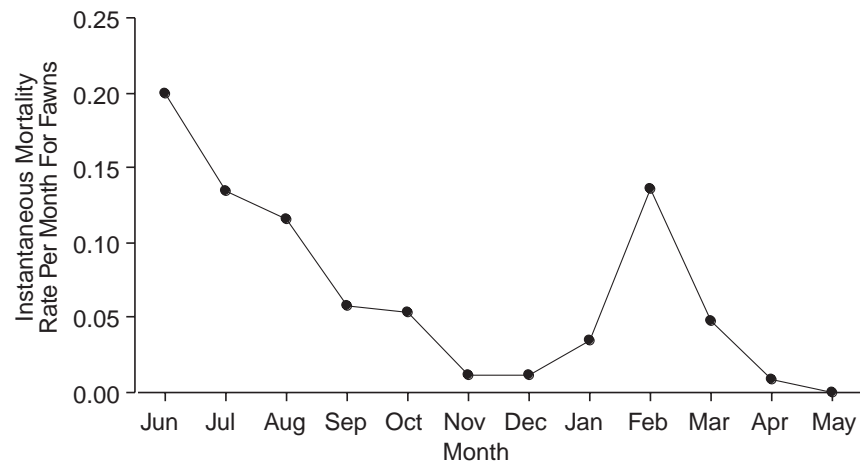
Figure 48.
Instantaneous monthly mortality rate for radio-collared mule
deer fawns in the Missouri River Breaks, 1976-1986 (after
Hamlin and Mackie 1989).

during 1980-86 to a high average 82 (35-91) percent for Cherry Creek whitetails between 1975 and 1987 (Dusek *et al.* 1989, Wood *et al.* 1989). An estimated 59 percent of potential white-tailed deer fawns was lost annually in the Swan Valley during 1976-79 (Mundinger 1981).

Although some extremes in average annual fawn mortality rates were observed in white-tailed deer, mule deer populations appeared to experience higher average and overall greater annual variation in fawn mortality. Mule deer fawn mortality ranged from a low average 60 (34-95) percent on Cherry Creek during 1976-86 to 65 (17-96) percent in the Missouri River Breaks during 1960-87

to 73 (55-97) percent on the northwest slope of the Bridger Mountains during 1973-87.

Total annual fawn mortality rates varied among the three mule deer study areas (Fig. 49). Summer-autumn fawn mortality rates were similar in level and trend among populations (Fig. 50); therefore variation in annual rates among areas resulted primarily from differences in overwinter mortality (Fig. 51). Average winter-spring mortality rates were lower than rates for summer-autumn and varied from 27 percent in the prairie-badlands to 33 percent in timbered breaks and 35 percent in the mountain-foothill environments. Years of
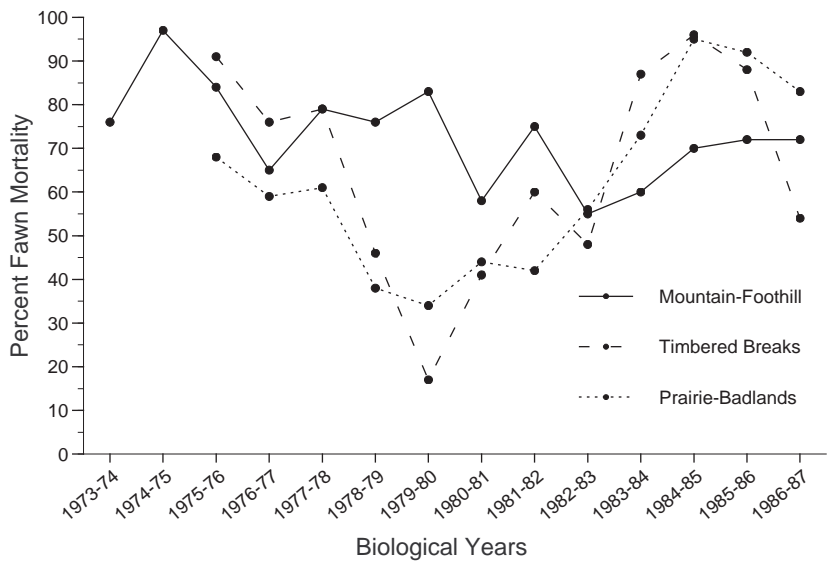
Figure 49. Comparative trends in total annual mortality of mule deer fawns in mountain-foothill, timbered breaks, and prairie-badlands environments, 1973-74 through 1986-87.
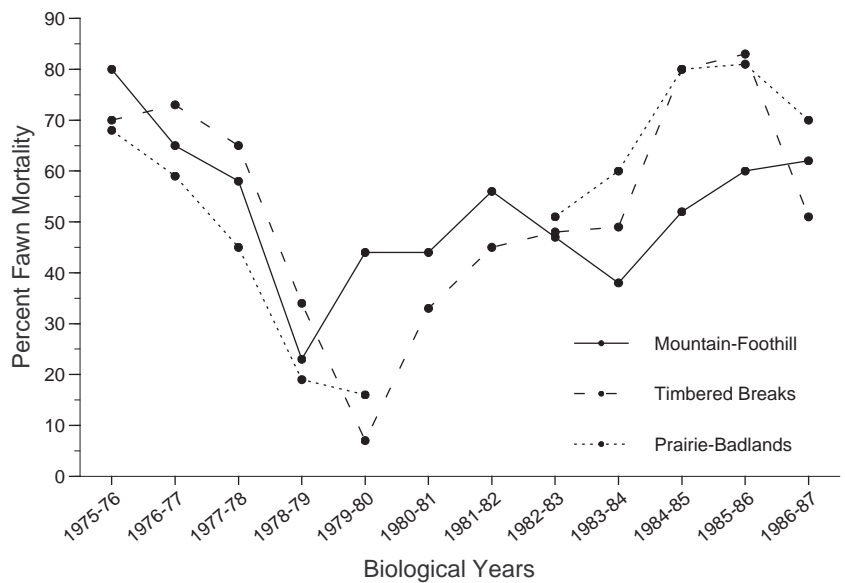
Figure 50. Comparative trends in mortality of mule deer fawns from June 1 through November 30 in mountain-foothill, timbered breaks, and prairie-badlands environments, 1975-76 through 1986-87.
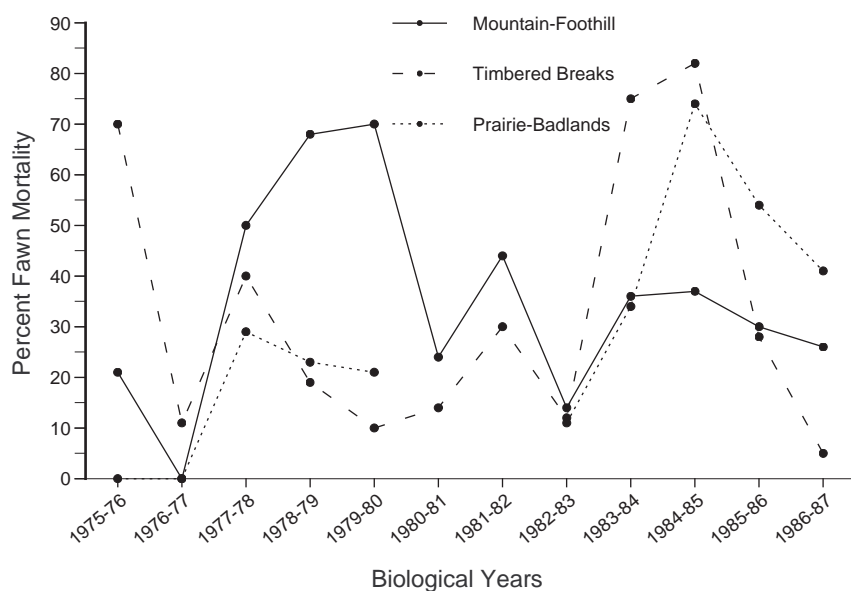
Figure 51.
Comparative trends in mortality of mule deer fawns from December 1 through May 31 in mountain-foothill, timbered breaks, and prairie-badlands environments, 1975-76 through 1986-87.
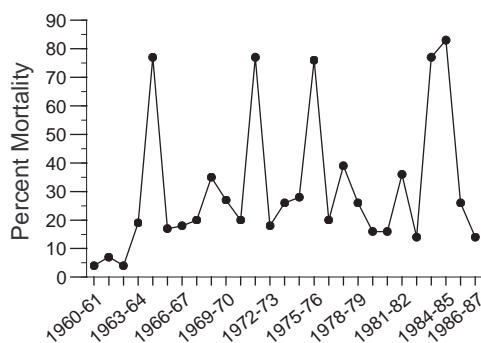
Figure 52.
Modeled trend in overwinter mortality rate for mule deer fawns in the Missouri River Breaks, 1960-61 through 1986-87.

high winter mortality in mountain foothill environments sometimes coincided with years of comparatively low fawn losses in prairie environments and vice versa. Apparently, summer-autumn mortality was influenced more by region-wide environmental conditions than was winter mortality. Winter mortality appeared to be influenced by complex interactions between specific populations and their local environments.

Both 1978 and 1979 winters were severe across the entire region, yet fawn mortality during 1979 was light to moderate in the prairie-badlands and timbered breaks populations but high in the mountain-foothill environment. Conversely, under moderate winter conditions following several years of drought, fawns experienced very high winter mortality on the plains during 1984-85, but only average mortality in the mountains. White-tailed deer fawns also experienced high mortality on Cherry Creek and relatively high mortality on the lower Yellowstone River during those drought years when adult female densities also were high (Dusek *et al.* 1989).

Moderate to high rates of overwinter fawn mortality were more common among mule deer in mountain environments. Populations in the Missouri River Breaks and other eastern Montana prairie-badlands habitats occasionally experienced episodes of extremely high mortality interspersed with several years of low mortality. This is clearly evident in trends in overwinter mortality of mule deer fawns in the Missouri River Breaks (Fig. 52). Over 27 years, beginning in 1960-61, there were 5 years in which overwinter mortality exceeded 77 percent. These included two "back-to-back" years of high mortality in the mid-1980s. More typically, however, years of high mortality were interspersed by 3-7 years of low to average mortality. Winters of intermediate fawn mortality were rare, suggesting that most often conditions predisposed entire cohorts either to survival or death. Subsequent population surveys, during 1988-1997 (Stivers unpubl.) indicate overwinter fawn mortality exceeding 80 percent also occurred during 1988-89 and 1994-95, continuing the long-term pattern of severe fawn losses at 5-8 year intervals.

Factors Affecting Fawn Mortality

In our studies, factors influencing fawn mortality varied widely such that the concept of a consistent "limiting factor" rarely applied. Differences between reproductive potential and recruitment

typically accrued from several sources and involved different patterns of fawn mortality.

In the Missouri River Breaks, predation was the single most important proximal mortality factor for fawns (Hamlin and Mackie 1989). During the 12-year period, 1975-87, predation by coyotes accounted for 88 percent of all deaths of radio-marked fawns and 85 percent of all known losses of fawns during summer and autumn. Coyote predation was also the proximate cause of death of almost all (95 percent) fawn mortality during winters 1976-86, though other factors were involved and predisposed some individual fawns to predation.

Despite the high incidence of predation, fawn mortality rates in the Missouri River Breaks were not significantly correlated with coyote density. Other factors, including population levels of alternative prey, yearlong habitat and forage conditions, and winter severity, influenced predation rates. This indicated that coyotes and predation, though important, were not always the overriding or ultimate factors affecting fawn survival. Rather, the importance of predation was tied to other biological and environmental factors that simultaneously influenced mortality.

Productivity and fawn survival to early winter in the Missouri River Breaks and elsewhere also were closely correlated with summer forage production and conditions during most years (Hamlin and Mackie 1989, Wood *et al.* 1989). Forage quality, as determined by the succulence of vegetation, and the timing and length of the period when green, succulent vegetation was available, appeared to be most important. Forage production and quality in the Missouri River Breaks were positively related to precipitation prior to the growing season and negatively to temperature during the early growing season (Hamlin and Mackie 1989).

The relationship between forage supply and fawn mortality in deer has been assumed to be density dependent; as deer numbers increase relative to

forage supply, fawn mortality rate is also expected to increase. We did not find evidence to support this concept, especially in terms of a compensatory relationship between winter population size or density and overwinter mortality and spring recruitment rates. Among mule deer, recruitment rate was significantly related to the number of adults in the population during spring only on the Cherry Creek area. However, it was also related to drought. For white-tailed deer, the number of mature females in the lower Yellowstone River population during spring also was significantly correlated with number of fawns recruited to the following spring. The limitation was behavioral and involved resource partitioning during summer rather than amount of forage available per capita (Dusek *et al.* 1989). There were no significant, positive linear relationships between numbers of mule deer and fawn mortality rate during summer-autumn or winter-spring on any area, nor was such a relationship evident for white-tailed deer on Cherry Creek. In the Missouri River Breaks where forage production was measured over 11 years, fawn recruitment was not related to relative deer density or the amount of forage per capita in the population (Hamlin and Mackie 1989). Rather the relationship appeared to be with forage quality or the length of time green, succulent forage was available.

Our findings concerning density and fawn survival do not imply that deer density is not involved or cannot

...fawn recruitment was not related to relative deer density or the amount of forage per capita in the population. Rather the relationship appeared to be with forage quality or the length of time green, succulent forage was available.

be a factor of some importance in fawn mortality. However, we documented no consistent density dependent relationships within limits of the variation in deer numbers and fawn mortality/recruitment rates observed. The only direct correlation we observed between deer numbers and mortality appeared to involve social rather than forage factors.

The effects of winter severity on fawn mortality appeared to be related to a complex of factors that influenced animal condition prior to, during, and following winter. In the Missouri River Breaks and Bridger Mountains, winter severity and fawn mortality during the same winter were positively related, but variation was high. Also, there were numerous exceptions such that predictability was limited (Hamlin and Mackie 1989, Pac *et al.* 1991). For example, fawn mortality during two of the most severe winters on record in the Breaks, 1977-78 and 1978-79, was less than half that recorded in other severe winters (Fig. 52). Conversely, winter severity was below the mean in 1983-84 and only slightly above average during 1984-85, when fawn mortality rates were among the highest recorded. Similar variation between winter severity and mortality occurred in the Bridger Mountains. There also were differences in winter severity-mortality relationships between populations in the

Bridgers (Pac *et al.* 1991). This variation indicated that winter mortality involved factors and interactions beyond simple winter severity.

Prior forage conditions, especially in the Missouri River Breaks, helped explain some of the anomalies in the relationship between winter severity and fawn mortality. In the Breaks, drought that resulted in below average forage conditions and early desiccation of vegetation during one or more years prior to a moderate or severe winter appeared to cause significant mortality; above-average forage conditions greatly tempered overwinter losses even in severe winters. Poor summer forage conditions prior to winter accentuated mortality through the winters of l964-65 and 1971-72 and apparently was the major factor in the heavy mortality that occurred through the winters of average severity in 1983-84 and 1984-85. Conversely, above average forage conditions preceding very severe winters in 1968-69, 1977-78, and 1978-79 put deer in very good condition and greatly reduced mortality through those winters.

Other studies have identified or implicated other factors that interact with predation, forage production, population density, and weather to influence overwinter mortality of fawns. For example, birth dates and weights of fawns can vary considerably from year to year. Later birth dates and/or reduced birth weight may, in turn, result in smaller fawns in poor condition or with limited body reserves in autumn. However, these variables that may predispose fawns to winter mortality are effects of environmental fluctuation rather than direct determinants of mortality rates.

Hunting mortality of fawns varied widely with regulations governing timing and take of antlerless deer, hunter selectivity, habitat security, and hunting pressure. Hunters usually selected against fawns during antlerless seasons. Harvest rate of fawns averaged 59 percent (43-78 percent) of the harvest rate of adult female mule deer in the Missouri River Breaks (Hamlin and Mackie 1989) and 60 percent (27-83

percent) of the harvest rate of adult female white-tailed deer on the lower Yellowstone River (Dusek *et al.* 1989). For mule deer, an average 12 percent (1-35 percent) of the estimated number of fawns on the Missouri River Breaks study area disappeared during autumn, about one-third (4 percent) of this mortality was associated with hunting. On the Cherry Creek area during 1982-86, a slightly higher 20 percent (0-45 percent) of the estimated number of mule deer fawns present in early autumn was lost through the hunting season. Average autumn mortality due to hunting was 8 percent. Hunters removed an average 12 percent (3-22 percent) of all white-tailed deer fawns on the lower Yellowstone River during autumn, 1980-85. Fawn harvest rates increased with hunting pressure, especially in association with availability of multiple antlerless permits.

Fawn deaths due to disease, abandonment, accidents, and traffic always occur and contribute to mortality patterns and rates. Because of low incidence, their individual and collective contributions to fawn mortality have rarely been monitored.

Adult Mortality

Once established as adults in a population, probability of survival is high and some consider mature deer relatively immune to all but the most extreme natural conditions, especially where large predators are not a threat. Yet the patterns and rates of adult deaths (or survival) can be equally as critical as recruitment to population characteristics, dynamics, and trends over time. Adult females and males have energy demands that are unique to their roles in the reproductive effort and result in different survival rates. Understanding these sex-related differences in mortality rates is essential in management to sustain quality populations and diverse hunting opportunities. Harvest management often assumes that hunting or harvest-related mortality replaces other forms of adult mortality, but both harvest and other mortality events and rates may operate and vary independently.

Adult Female Mortality

Natural mortality rates were low and generally similar across environments (Tables 5 and 6). Total annual mortality in the Bridger Mountains for adult female mule deer was 12 percent during 1973-86 (Pac *et al.* 1991). During summer-autumn, adult female mortality from all causes in this mountain-foothill environment averaged only about 5 percent (range = 0-11 percent) with natural and hunting mortality each

Harvest management often assumes that hunting or harvest-related mortality replaces other forms of adult mortality, but both harvest and other mortality events and rates may operate and vary independently.

Table 5.
Average and range in total, hunting, and natural mortality rates[a] for adult (≥1 year) female mule deer in three Montana environments.

Environment	Total Annual Mortality	Hunting Mortality	Natural (Non-hunting) Mortality
Mountain-Foothill[b] N = 14 years	0.121 (0.083)[c] range 0.000-0.286	0.048 (0.031) range 0.000-0.111	0.073 (0.065) range 0.000-0.236
Timbered Breaks[d] N = 26 years	0.172 (0.090) range 0.022-0.430	0.110 (0.075) range 0.000-0.298	0.062 (0.047) range 0.014-0.248
Prairie-Badlands[e] N = 5 years	0.254 (0.166) range 0.003-0.420	0.210 (0.153) range 0.001-0.370	0.050 (0.045) range 0.000-0.120

[a] Calculated from arithmetric models that reconciled successive population estimates with data on population composition, recruitment, and marked deer mortality rate.

[b] Pac *et al.* (1991).

[c] Average (std. dev.)

[d] Hamlin and Mackie (1989).

[e] Wood *et al.* (1989).

Table 6.
Annual survival rates and cause-specific mortality rates for yearling and older female white-tailed deer under different harvest regimes in three Montana environments.

		Survival		Mortality Hunting	Mortality Natural(Non-hunting)
	Age	Rate [a]	95% C.I.	Rate [a]	Rate [a]
Northwest Montane Forest [b]					
1989-1995 (low harvest)	≥ 1 yr.	0.843	0.809-0.878	0.058	0.099
Plains Riverbottom [c]					
1980-1984 (low to moderate harvest)	1 yr.	0.830	0.690-0.990	0.050	0.120
	≥2 yrs.	0.680	0.590-0.790	0.200	0.110
1984-1988 (high harvest)	1 yr.	0.430	0.230-0.800	0.330	0.240
	≥2 yrs.	0.450	0.360-0.570	0.390	0.160
Prairie-agricultural [c]					
1984 (moderate harvest)	≥2 yrs.	0.800	0.660-0.970	0.160	0.040
1984-1987 (high harvest)	≥2 yrs.	0.660	0.530-0.830	0.290	0.050

[a] Calculated using Micromort program (Heisey and Fuller 1985)
[b] Sime, unpublished data
[c] Dusek *et al.* (1992)

accounting for about half of the losses. During winter-spring, the average female mortality rate was 7 percent (range = 0-24 percent).

Females in the Missouri River Breaks had an average annual mortality rate of about 17 percent (2-43 percent), 11 percent occurred in summer-autumn and 6 percent over winter, during 1960-86 (Hamlin and Mackie 1989). The difference in annual mortality between these two environments was due to greater hunter harvest of females in the Missouri River Breaks. Natural mortality was very similar in the two environments (Table 5).

Although coyote predation on adult females was low, it was the major known natural mortality factor and the second leading cause of death overall in the Breaks; predation was also suspected to be at least the proximal factor in most losses of unknown cause. Coyote predation on adults was highest during winter and spring and included individuals in good as well as poor condition (Hamlin and Mackie 1989). Although coyotes and/ or other predators occurred on all study areas, we did not determine the incidence of predation relative to other natural mortality factors on adult females in other populations during the studies.

Hunting was the major known cause of death among adult female mule deer in all but the Bridger Mountains where natural mortality accounted for about three-fourths of the total. Hunting mortality varied with season type and bag limits for antlerless deer.

The lowest average annual mortality rate for adult females occurred in the Bridger Mountains where relatively conservative hunting regulations and other factors limited harvest to an average 4.8 percent of preseason numbers (Table 5). In the Missouri River Breaks total annual mortality of females averaged 17 percent over a 26-year period. This included annual mortality averaging 22 percent during 13 years of 2 deer-either sex seasons, 17 percent during 6 years with 1 deer-either sex hunting with some additional antlerless licenses, and 7 percent for 8 years in which only males could be taken on general licenses. On the Cherry Creek area, annual hunting mortality rates for adult females averaged 21 percent during 1982-86, but increased progressively from 1 percent during a 1 deer-either sex season to 9 percent with 1-deer either sex plus limited antlerless permits and 32 percent (27-37 percent) when multiple licenses for antlerless deer were available to hunters (Wood *et al.* 1989).

Hunting was the major known cause of death among adult female mule deer in all but the Bridger Mountains where natural mortality accounted for about three-fourths of the total.

Long-term trends in overwinter and total annual mortality of adult females in the Missouri River Breaks (Fig. 53) illustrate the variability in female mortality rates and the downward trend in total annual mortality associated with reduced hunting mortality after 1975. These data also document unusually high incidences of mortality among adult females during 1961-62 and 1971-72. Similar high total and overwinter mortality exceeding 40 percent apparently occurred during 1994-95 (Stivers unpubl.).

The high annual mortality rate for adult females during 1961-62 was not associated with overwinter mortality, but with heavy harvest rates of females promoted by special harvest regulations and environmental conditions that increased vulnerability of deer to harvest that year. The extreme mortality during winter 1971-72 occurred at a high female population when dry conditions reduced the quantity and quality of forage produced during the previous summer. This event occurred after a long series of years of relatively heavy harvest of adult females (Fig. 53).

Among whitetail populations, non-hunting mortality rates of females were low to moderate (≤ 16 percent). Mature females experienced average hunting mortality of 6 percent in the northwestern montane forest environment where relatively conservative hunting occurred. This compared with harvest rates of 16-39 percent in the prairie-agricultural and plains riverbottom environments (Table 6).
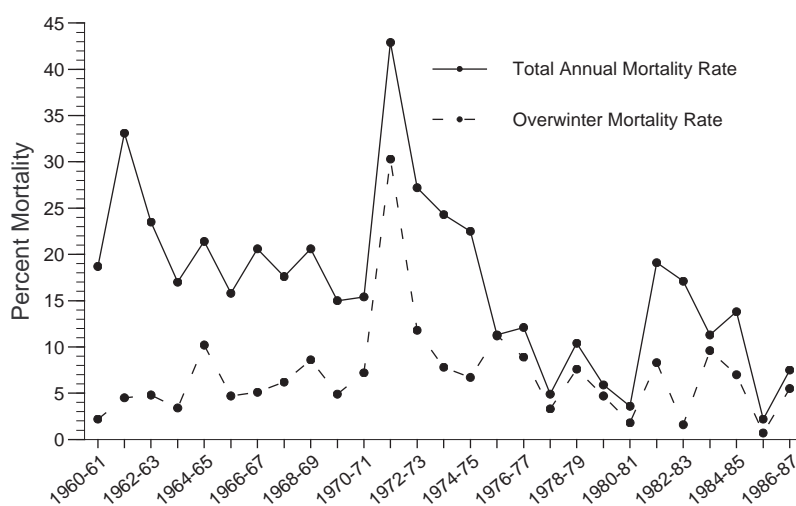
Figure 53.
Trends in total annual and overwinter mortality rates for adult female mule deer in the Missouri River Breaks, 1960-61 through 1986-87.

In both species and across all study areas hunting mortality had little, if any, measurable effect on natural mortality rates of adult females. Thus, our findings do not support the concept that mortality from hunting would replace that from other causes. Perhaps the low levels of natural mortality that characterized adult females in all of our studied populations may have represented base levels of mortality that could not be substantially reduced (Dusek *et al.* 1992). We conclude that opportunities to substitute harvest for individuals that might otherwise die from other factors is limited. Consequently, the death of one adult female would not increase the probability that others would survive, and hunting losses became additive to overwinter and other natural mortality.

Where hunting mortality of adult females is low (Pac *et al.* 1991), relatively large numbers of adult females may occur in older, more vulnerable age classes. When severe winters occur in such areas, higher than usual overwinter mortality of adult females may result. Such mortality is not necessarily related to forage availability, but rather to decreased energy reserves and physical condition associated with old age. Although heavier hunting may have removed some of these vulnerable deer, hunting mortality tended to be biased toward younger rather than old age classes.

We also determined differences in mortality rates among adult females related to habitat-use strategy and home range characteristics. Females establishing yearlong residency in areas of low topographic relief in the Missouri River Breaks experienced significantly higher mortality than either females resident to home ranges in steep terrain with north- and south-facing slopes or females that migrated annually to winter in steeper terrain (Hamlin and Mackie 1989). As numbers of adult females increased in the population, greater numbers inhabited drainage heads and along ridgetops on home ranges with low topographic relief. This may have served to predispose these females to very high mortality during years of extremely dry

summer and/or severe winter conditions such as 1971-72 and 1994-95. Relatively few adult females remained in areas of low relief following episodes of significant overwinter mortality (Hamlin and Mackie 1989).

Adult Male Mortality

As noted earlier, adult males were outnumbered by females in all populations. This reflects higher mortality of males associated with hunter selection for males as well as differences in biology and behavior of the sexes.

We found that males rarely lived more than 7-8 years. Hunters selected for older, larger antlered males over younger, smaller individuals. Also, where they occurred, males over six years of age appeared particularly vulnerable to mortality during severe winters. As dominant breeders, most of these older males entered winter in poor physical condition. Yearling males were also vulnerable to mortality during severe winters. As with fawns, yearling males apparently emphasize body growth over accumulation of fat reserves, and many are unable to survive the energy deficits associated with long periods of cold and utilization of low quality forage.

In our studies, adult males experienced mean annual mortality rates ranging from 41 to 61 percent, more than twice the rates experienced by adult females (Table 7). Average rates and variation were similar for the two species. Annual mortality rates varied widely within and among individual populations from a low 18 percent to a high 80 percent. Both the highest and the lowest annual rates were recorded for mule deer in the Bridger Mountains.

Hunting was the major cause of mortality for adult males of both species in all environments. Among populations, mean annual hunting mortality rate ranged from 33-58 percent of estimated pre-hunting season populations. Within individual populations, annual variation in hunting mortality was greatest in the Bridger Mountains where rates varied from 14-70 percent (Table 7).

Despite greater vulnerability and more uniform distribution across populations and habitats, hunting mortality rates for yearling males were generally lower than rates for older males, and smaller antlered (spike) yearling males were harvested at a lower rate than larger antlered (2-point) yearlings. In the Missouri River Breaks yearling males were harvested at an average rate of 36 percent compared to 53 percent for older adults (Hamlin and Mackie 1989). On the lower Yellowstone River, hunters harvested males ≥ 2 years in greater proportion than their occurrence in the population, while the relative proportion of yearling males taken decreased with smaller antler size (Dusek *et al.* 1989). Spike antlered yearling males apparently were selected against or undetected by hunters in all areas.

The relatively low rates of overwinter mortality for adult males suggested that hunting mortality may substitute for natural mortality to a greater degree among adult males than it does among females. With the high harvest rates for adult males in most populations, a greater proportion of these animals (e.g.. older,

Table 7.
Total and cause-specific annual mortality rates[a] for adult (≥1 year) male mule deer and white-tailed deer in four Montana environments.

Environment	Total Annual Mortality	Hunting Mortality	Natural (Non-hunting) Mortality
MULE DEER			
Mountain-Foothill[b] N = 14 years	0.460 (0.145)[c] range 0.182-0.800	0.404 (0.160) range 0.143-0.700	0.056 (0.081) range 0.000-0.257
Timbered Breaks[d] N = 26 years	0.414 (0.109) range 0.217-0.609	0.375 (0.112) range = 0.150-0.580	0.038 (0.024) range = 0.000=0.114
Prairie-Badlands[e] N = 5 years	0.612 (0.065) range 0.520-0.700	0.584 (0.064) range 0.480-0.650	0.036 (0.023) range 0.000-0.060
WHITE-TAILED DEER			
Plains Riverbottom[f] N = 6 years	0.600 (0.070)	0.550 (0.070)	0.060 (0.020)
Northwest Montane Forest[g] N = 6 years	0.419 (0.019)	0.328 (0.018)	0.091 (0.032)

[a] Calculated from arithmetic models that reconciled successive population estimates with data on population composition, recruitment, and marked deer mortality rates on all areas except the Northwest Montane where rates were calculated using Micromort (Heisey and Fuller, 1985).

[b] Pac *et al.* (1991).

[c] Average (std. dev.).

[d] Hamlin and Mackie (1989).

[e] Wood *et al.* (1989).

[f] Dusek *et al.* (1989).

[g] Sime, unpubl., representing mortality rates calculated across the span of years.

predation by coyotes, mountain lions, and possibly bears. Adult females, conversely, selected home ranges that provided for isolation and security from predation. Evidence from recent studies in the Bridger Mountains (Pac, unpubl. data) suggests that predation by both coyotes and mountain lions may be greater than previously believed or has increased recently and is sufficient to influence survival of males of all age classes.

Emigration and Immigration

Dispersal is the movement of (young) animals from their natal or a subsequently established home range. Dispersal movement culminating beyond boundaries of a population we call emigration. Movement of deer from adjacent populations into a population we studied was immigration. Immigration and emigration represent special gains and losses (i.e., recruitment and mortality) of adults in population dynamics. Immigration and emigration also may be viewed as a mechanism for redistribution of individuals, especially young males, for genetic interchange and resource partitioning (Dusek *et al.* 1989, Hamlin and Mackie 1989, Pac *et al.* 1991). In some mammals, redistribution of individuals between established populations has been reported to influence reproductive potential through disruption of social structure and stress effects (Bailey 1969).

Most deer populations, including all we studied, were surrounded at least in part by habitat to or from which deer could move. In most areas, we were only able to measure emigration. Immigration was rarely detected directly and was evident only because population data did not indicate annual declines associated with emigration.

Emigration and immigration rates varied within and among populations and habitats. Emigration rates were strongly sex and age related. Relatively high

dominant breeding males destined to die over winter) are harvested. Lower harvest rates during many years, especially those following extremely dry summers and/or preceding severe winters might not result in appreciably lower total annual mortality rates. Gavin *et al.* (1984) reported that adult male Columbian white-tailed deer experienced 40 percent annual mortality even in the absence of hunting.

Data for white-tailed deer on the lower Yellowstone River also indicated that hunting mortality compensated for natural mortality because few males >4 years of age survived to be predisposed to natural mortality. Based on annual mortality rates observed, only 26 (3 percent) of 1000 yearling males would be expected to live to 5 years when the cumulative energetic cost of breeding could lead to overwinter mortality. This compared with a similar cohort of 1000 yearling females, from which 370 (37 percent) would be alive after 5 years, and 175 (18 percent) would be expected to live to 8 years.

Our intensive studies through 1987 did not directly detect predation as an important mortality factor on adult males of either species in any environment. However, resource partitioning and habitat segregation between the sexes often resulted in male home ranges located in local environments frequented by and possibly conducive to successful

The relatively low rates of overwinter mortality for adult males suggested that hunting mortality may substitute for natural mortality to a greater degree among adult males than among females.

rates of emigration were recorded among young mule deer only on the Missouri River Breaks and Cherry Creek areas and for white-tailed deer on Cherry Creek. Emigration was uncommon among mule deer in Bridger Mountain populations, especially among females on the west slope. Emigration was recorded but appeared rare among whitetails marked in the Swan Valley (Mundinger 1980).

Where it occurred, emigration was greatest and most consistent among young males; emigration of females was comparatively low and more variable. Emigration centered in yearlings, with only occasional incidence among 2- and 3-year old males and females or >8-year old females.

Relatively high rates of emigration averaging 51 percent (27-78 percent annually during 1976-85) among yearling male mule deer in the Missouri River Breaks apparently were balanced by nearly equal immigration by young males from adjacent areas (Hamlin and Mackie 1989). Even higher rates (ave. 67 percent) of emigration among yearling mule deer males in the prairie-badlands environment also appeared to be largely compensated by immigration; though slight declines in numbers of yearling males on the area through summer suggested a possible net loss of adults from these movements (Wood *et al.* 1989).

The more variable rates of emigration by young females may have been influenced by matriarchal aggression and population density, and apparently were not balanced by immigration. In the Missouri River Breaks, most female emigration (ave. = 27 percent) from the study area occurred at low population levels, among yearlings in the first two, numerically large cohorts recruited following the population low in the mid 1970s (Hamlin and Mackie 1989). This was similar to the "pre-saturation" dispersal proposed by Lidicker (1978), and it served to promote rapid filling of vacant habitat and irruptive population growth in the patchy environment. Annual emigration rate of yearling

females was ≤10 percent during most other years. However, net emigration involving possibly 25 percent or more of the yearling females from the 1986 cohort apparently occurred between spring and December 1987 (Hamlin and Mackie 1989). This followed the highest adult female density ever recorded on the area, and may have represented a form of "saturation" dispersal (Lidicker 1985) following the filling of most suitable reproductive habitat in the area by the increasing numbers of females during the late 1970s-mid 1980s.

Emigration of yearling, 2- and 3-year old female mule deer was very low in the Cherry Creek population and must have been balanced by immigration (Wood *et al.* 1989). In the Bridger Mountains, emigration of females was very rare and unimportant in dynamics of west slope populations. Greater numbers of young females emigrated from populations on the east slope, but this also was unimportant in population dynamics.

Data for white-tailed deer in river bottom and prairie-agricultural environments indicated relatively high rates of dispersal of yearlings from natal home ranges, but variable rates of emigration from natal populations (Dusek *et al.* 1989, Wood *et al.* 1989). On the lower Yellowstone River, nearly half (46 percent) of all males marked as fawns and monitored for 18 months or more dispersed from natal home ranges, primarily to establish new ranges up or down the river bottom. However, very few left the river bottom. A similar pattern of dispersal was evident for young females of which 17 percent dispersed to establish home ranges elsewhere on the river bottom (Dusek *et al.* 1989). Limited data from marked white-tailed deer and a high net loss of adults during summer suggested a high rate of emigration for young females as well as males from the Cherry Creek population (Wood *et al.* 1989).

Overall, emigration did not appear to occur in either a manner or to an extent that it would singly control deer numbers in any population. Rather, as in the

Overall, emigraton did not appear to occur in either a manner or to an extent that it would singly control deer numbers in any population.

Missouri River Breaks, it was one of many factors that at times limited population growth below numbers that may have occurred based on fawn recruitment (Hamlin and Mackie 1989). There, and perhaps in other areas, the most important role of dispersal and emigration may be as a mechanism to maintain deer in available habitat, allocate resources by sex and age, and promote the genetic and behavioral diversity necessary to sustain populations over time.

Patterns of Population Growth and Fluctuation

Deer experience two distinct phenomena in population dynamics: (1) a period of population growth associated with colonization or reestablishment in new or vacant habitats, and (2) post-establishment fluctuations and changes in population size and composition influenced by population-habitat relationships, environmental variation, and management. Where minimum adaptation is required and recruitment and dispersal are high, initial population growth may be rapid, in an eruptive pattern, at least during the early stages of development. Where substantial adaptation and specialized movements are necessary to access and effectively utilize all habitat, or recruitment and female dispersal are limited, deer will colonize slowly and population growth may be relatively gradual.

Once established, all deer populations fluctuate over time. Such fluctuation varies among populations in response to the specific conditions that exist in each area. Although, at times, populations of both species may appear to fluctuate in synchrony, we found deer numbers and dynamics to vary independently between species and study areas. The more similar the environments and conditions, the less the difference in the pattern, timing, and magnitude of population fluctuation.

We studied established populations, so we had only limited opportunity to study early development and growth phases of populations. Data on population growth were obtained primarily during periods of recovery from low population levels. Other long-term deer population studies (e.g., McCullough 1979) that provide the basis for current concepts about population dynamics have focused primarily on the process of population growth.

We recognized four types of population change over time: general, long-term changes in distribution and demographics; periodic fluctuations spanning several years; year-to-year fluctuations; and season-to-season changes within years.

Long-term changes in abundance can occur at landscape, ecosystem, or population levels. Mule deer increased from scarcity in most areas of Montana to abundance throughout the state during the 1940s-1960s (Egan 1971). Since the
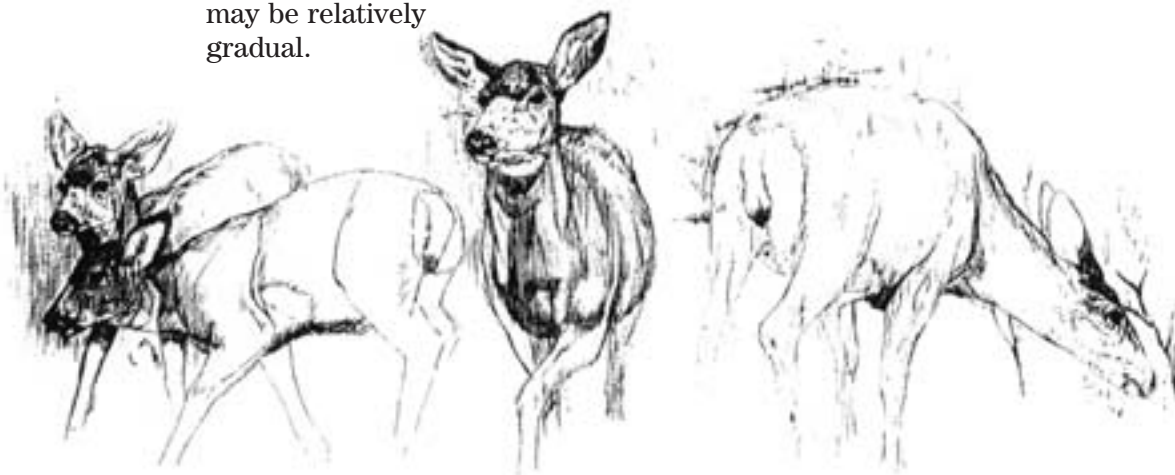
mid to late 1960s populations have declined in many areas, especially in western and southern mountain-foothill environments, while numbers have increased in plains habitats (Mackie *et al.* 1985, Eustace 1988).

White-tailed deer have gradually increased and spread throughout most of Montana since the 1930s and 1940s (Allen 1971). Present whitetail populations may represent all-time highs in both distribution and abundance for the species in the northern Great Plains and Rocky Mountains (Mackie *et al.* 1985, Dusek *et al.* 1989). We found no evidence of direct competition leading to replacement of one species by the other. However, regional buck harvest trends, especially for southern and southwestern Montana, suggest continuous spread and increases in numbers of whitetails since the mid 1970s, while mule deer have declined from 1960-1975 levels (MFWP Wildl. Div. 1995, Hamlin and Erickson 1996). Such trends may be indicative of changes in relative abundance of the two species in areas where whitetail populations have developed or expanded in the wake of environmental changes and conditions favorable to the species (Eustace 1988, Dusek *et al.* 1989), while mule deer numbers have declined, especially in their stronghold, mountain-foothill habitats.

Long-term trends in distribution and abundance in specific habitats include deer responses to changes in land use. Long-term trends also reflect subtle responses to changes in climate and weather conditions, the distribution, abundance, and behavior of predators and other wild animals, and the presence and activities of man. Thus, trends may be difficult to detect, and cause-effect may be impossible to isolate or quantify.

For our study areas, data were available to quantify population fluctuations over periods of 6 to 28 years. In the Missouri River Breaks, additional data were available to generally estimate early population growth and subsequent fluctuations in numbers of mule deer from the late 1930s to 1960 when more intensive studies were initiated (Hamlin

and Mackie 1989). Aerial surveys during winter and/or early spring, 1988-1995 (Stivers unpubl.) provided data to generally estimate population trends following termination of intensive studies in 1987. Collectively, these data provided estimation of population trend from the 1930s through 1995 (Fig. 54).

These data, together with various reports (Hamlin and Mackie 1989), suggested that the present population on the Missouri River Breaks study area developed from a small number of mule deer remaining on the area during the 1930s (Fig. 54). Mule deer numbers apparently increased progressively from 1938 or 1939 through 1947-1948 in a pattern similar to irruptive or introduced populations (Caughley 1970, McCullough 1979, 1983). After 1948, the population fluctuated frequently and often widely, between years and over periods of years in relation to patterns of recruitment and adult mortality. Trends in spring populations during the 27-year period of intensive studies from 1960-61 through 1986-87 (Fig. 55) indicate the relative contributions of recruitment and adult mortality.

Even in these long-term data sets, interpretation of pattern in long-

term trends can vary depending upon perspective and any additional population data available and applied to analysis. One perspective might interpret the long-term trend to reflect annual and periodic fluctuations of variable amplitude around a long-term mean, or average population size. A second could suggest periodic fluctuations within a long-term trend of generally increasing deer numbers from the early 1960s through the early 1990s. A third perspective might point to fluctuating, but generally decreasing numbers from the initial peak in the

...long-term trends in mule deer numbers in the Missouri River Breaks do not support the view that a population, after declining from an initial peak, never recovers to that high.
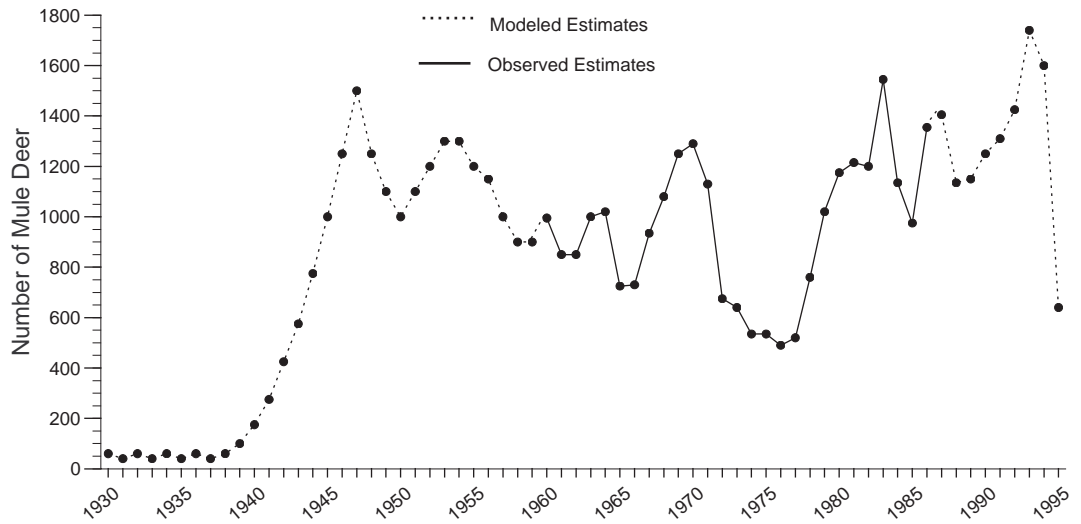
Figure 54.
Estimated numbers of mule deer on the Missouri River Breaks study area during early winter 1930-1995.
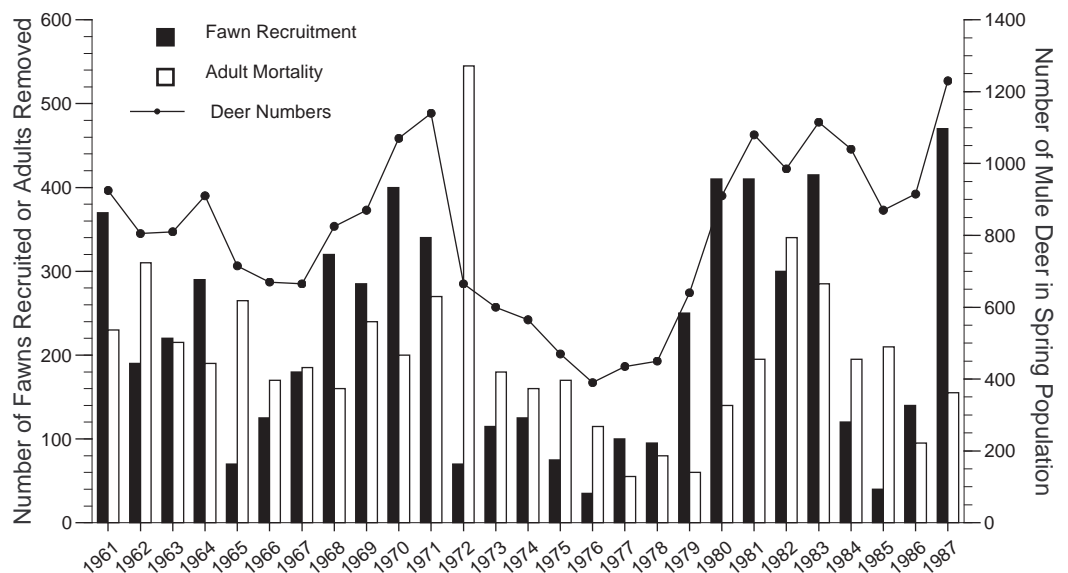
Figure 55.
Spring population trend in relation to fawn recruitment and adult mortality for mule deer on the Missouri River Breaks study area, 1961-1987.

late 1940s through 1976-77, followed by generally increasing numbers from 1977 through the early 1990s. Still a fourth view might suggest that trends reflect periodic, cycle-like fluctuations, influenced by population and proximal environmental factors. Within the long-term data set, trends for any combination of two years or more could provide numerous interpretations or conclusions depending upon such chance events as the particular year selected to begin and the total number of years involved (Hamlin and Mackie 1989). It should also be noted that regardless of perspective and interpretation, long-term trends in mule deer numbers in the Missouri River Breaks do not support the view that a population, after declining from an initial peak, never recovers to that high.

Current mule deer populations in the Bridger Mountains and on the Cherry Creek area also developed during the 1940s and 1950s (Wilkins 1957, Wood *et al.* 1989), either as a result of increases among small numbers of deer that existed in these areas or by colonization from other habitats. Because data on early growth were lacking, our findings

documented fluctuations and trends only after populations had become established and declined from early "peaks."

In the Bridger Mountains, mule deer "…were quite scarce and infrequently seen" as late as 1948, while a "large population" was evident by the mid-1950s (Wilkins 1957). Data obtained during 1972-75 compared with 1955-56 suggested a possible population decline of 50-67 percent by the time our intensive population studies were initiated (Hamlin 1977). Our data provided detailed estimates of population size and trend relative to recruitment and adult mortality for mule deer on the Northwest Slope from 1972 through 1987 (Fig. 56) (Pac *et al.* 1991) and more general estimates during 1988-97 (Pac unpubl. data).

There was no evidence, either from trends in estimated mule deer numbers in individual populations or from more general population surveys through 1995-96, of long-term increase or decrease in populations in the Bridger Mountains since 1974. Although periodic fluctuations spanning several years appeared large to hunters and public perceptions of deer abundance, they
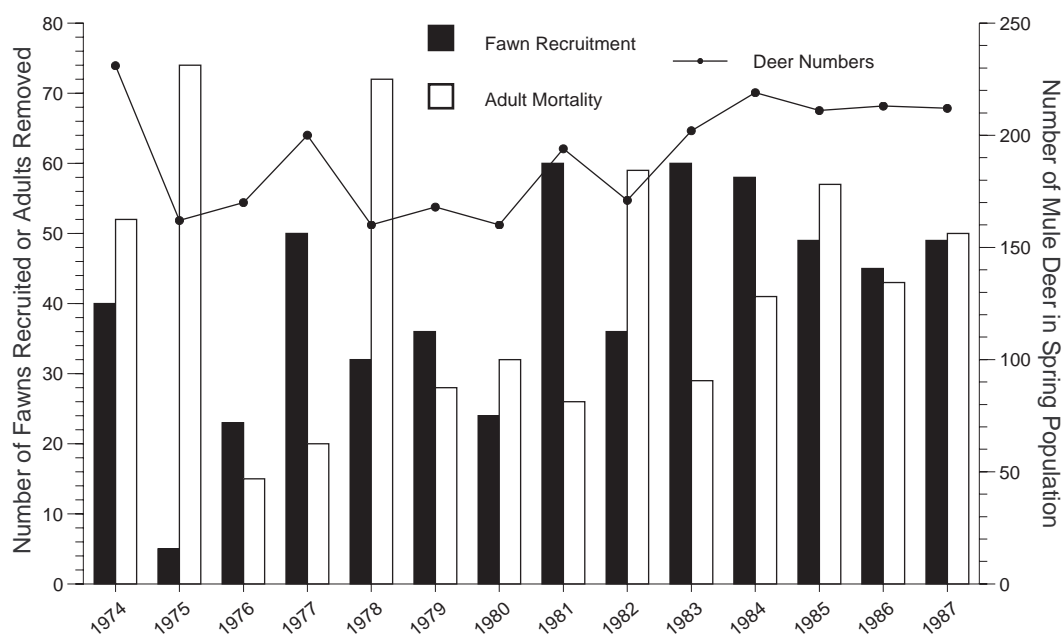
Figure 56.
Spring population trend in relation to fawn recruitment and adult mortality for mule deer associated with the Armstrong Range, Northwest Slope, Bridger Mountains, 1974-87.

seldom exceeded a 65 percent change in numbers. It appeared that the Bridger Mountain populations, dominated by long-lived adult females and low annual recruitment (Pac *et al.* 1991), were less likely to experience the wide fluctuations observed in mule deer populations in the Missouri River Breaks and other habitats.

No data were available concerning specific population characteristics or trends on the Cherry Creek area prior to 1975. However, if mule deer trends on this area were similar to southeastern Montana as a whole, harvest data (MFWP Annual Hunting and Harvest Reports, Wildl. Div., Helena.) would suggest that the population increased to an initial peak during the early 1960s. It subsequently fluctuated through a low in the mid 1960s to a second, possibly higher, peak during the early 1970s, and declined sharply to another low in 1975 (Wood 1987). During this study, surveys were completed and population estimates relative to recruitment and adult mortality were calculated only during 1975-1987 when mule deer numbers again cycled from a low through a peak in 1983-84 to still another low by 1986-87 (Fig. 57).

Relative changes in populations of mule deer in the three broadly different environments were measured only during 1975-1987 (Fig. 58). Again, although some synchrony was evident in pattern and timing of changes in the three populations, each fluctuated in a different manner and at a slightly different rate.

Greatest fluctuation in annual population levels occurred on the Cherry Creek Area, where mule deer numbers at their peak in 1983 were 600 percent higher than the low in 1976, then declined by more than 75 percent to another low in 1987. Conversely, population size varied only slightly in populations in mountain-foothill habitat where mule deer numbers on the northwest slope also increased, but were only 68 percent higher in 1984 than at the low in the mid-1970s. Further, they did not decline significantly during the mid 1980s, and they increased to an even higher peak in 1991.

The fluctuation in numbers in timbered breaks habitat was intermediate between mountain-foothill and prairie-badlands environments. Mule deer numbers on the Missouri River Breaks study area increased about 250 percent from 1977 to 1983, declined slightly during 1984-86, then increased again in 1987 (Hamlin and Mackie 1989).

The Cherry Creek and perhaps other mule deer populations in southeastern Montana plains habitats may be characterized by extreme "boom and bust" dynamics and trends over time. Locally, however, trends may also be influenced by specific environmental conditions, deer population structure, and harvest strategies. Deer surveys on lightly-hunted, surface-mined, and urban habitats in the vicinity of Colstrip indicated more or less steady population growth from 1979-80 to the early 1990s (Fritzen 1995); there was no evidence of severe decline similar to that on the Cherry Creek area during 1984-87.

Long-term census data to quantify growth and development of individual populations were lacking for white-tailed deer. Historical populations in eastern Montana were largely extirpated during the late 1800s, and whitetails
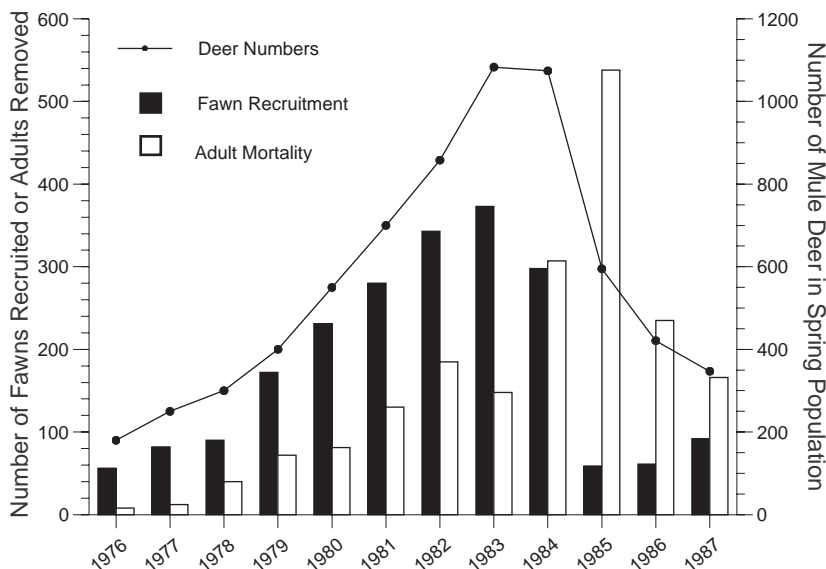
Figure 57.
Spring population trend in relation to fawn recruitment and adult mortality for mule deer on the Cherry Creek study area, 1976-1987.
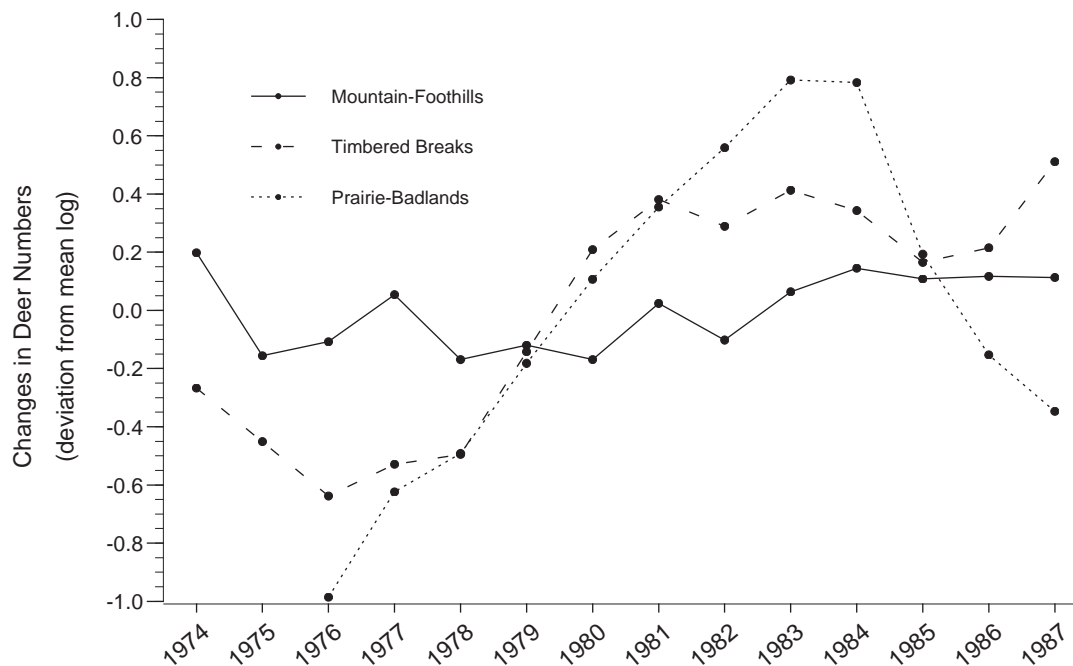
Figure 58.
Comparative annual changes in mule deer numbers in three Montana environments during spring, 1974-1987.

For both species, greatest fluctuations were in open, patchy, and variable environments; the least fluctuations were associated with more diverse, relatively stable habitats.

became reestablished on bottomlands along the Yellowstone River and upland prairie-agricultural environments only during 1940s and 1950s (Dusek *et al.* 1989, Wood *et al.* 1989). On the other hand, the species apparently was well established in the Swan Valley and other coniferous forest habitats in northwestern Montana prior to and following settlement. Reports indicated abundant populations there in the early 1900s, increases to early peaks in the mid-1950s, and general declines by the early 1970s (Arno *et al.* 1987) when our studies began. Thereafter, harvest records from questionnaire surveys and population estimates (MFWP unpubl.) indicate that white-tailed deer numbers gradually increased through the mid 1990s.

Comparative post-season numbers and trends in the three whitetail populations during years for which population estimates are available showed that each population changed differently (Fig. 59). For the Swan Valley, minimum population estimates (constructed using harvest-based models, Riley, pers comm.) indicated a gradual increase of about 44

percent in white-tailed deer numbers from 1975-76 to 1984-85 followed by a slight decline to 1986-87. Maximum estimates suggested continuous population increase to an approximate doubling of the population between 1975 and 1987. By comparison, white-tailed deer numbers on the lower Yellowstone River populations increased by 54 percent from 1980 to 1983-84 before decreasing to near-1980 levels by 1986-87.

Numbers of whitetails on the Cherry Creek study area were relatively stable during 1975-78, approximately doubled from 1979 to 1983, then declined by 91 percent to about one-fourth of the previous low in 1986-87. Although white-tailed deer and mule deer fluctuated somewhat similarly, whitetail numbers peaked and began to decline one year earlier than mule deer numbers (Fig. 60). For both species greatest fluctuations were in open, patchy, and variable environments; the least fluctuations were associated with more diverse, relatively stable habitats.
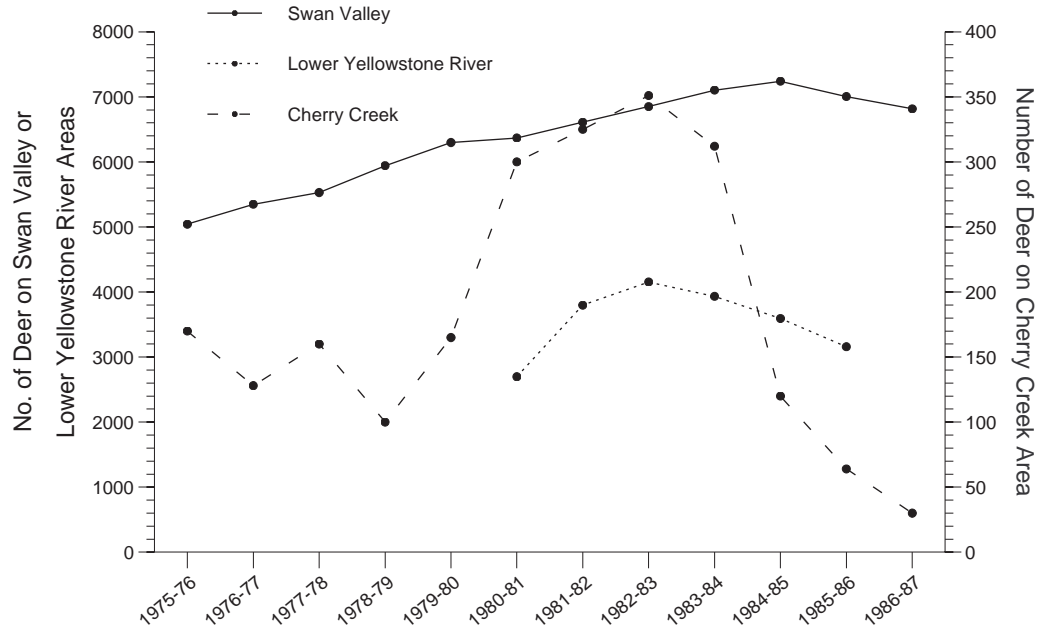
Figure 59.
Comparative population trends for white-tailed deer on Swan Valley, Cherry Creek, and Lower Yellowstone River study areas during early winter, 1975-76 through 1986-87.
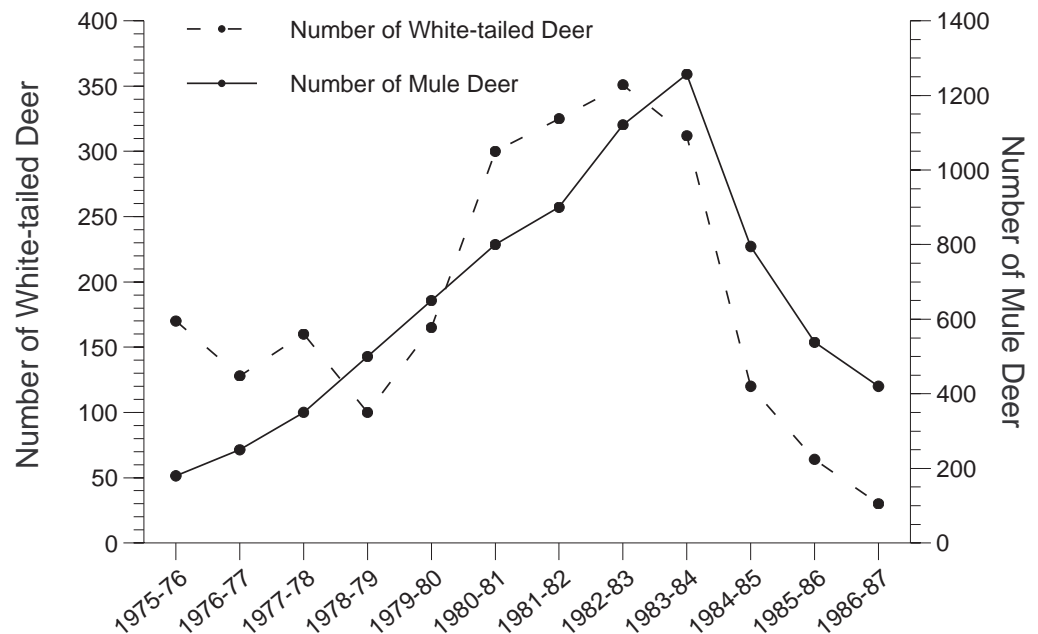
Figure 60.
Comparative trends in total numbers of mule deer and white-tailed deer on the Cherry Creek study area during early winter 1975-76 through 1986-87 (after Wood 1987, Wood et al. *1989).*

Management
Implications
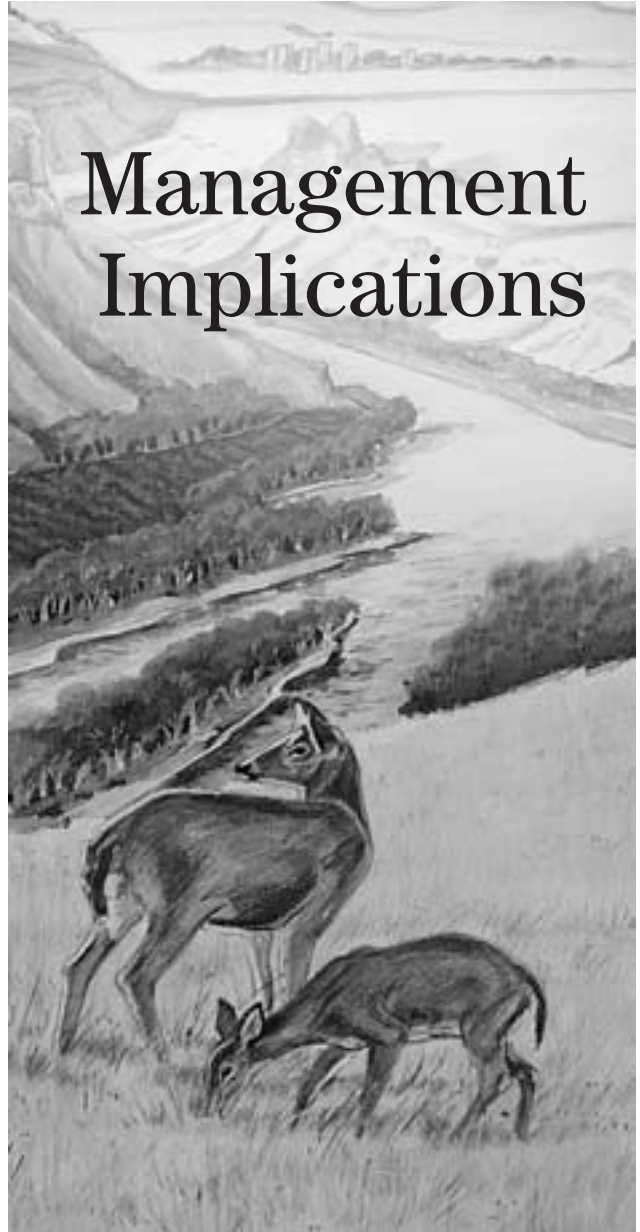
Traditional Concepts

Management of mule deer and white-tailed deer in Montana during the 1930s through the mid-1970s was based on the theory of range "carrying capacity", which related deer numbers to the amount of forage available in winter. This concept originated primarily in animal science and husbandry of domestic livestock in a simple, controlled management system. Although defined in essentially the same way, it was applied to free-ranging deer in complex ecological systems.

It seems easy to critique and criticize early wildlife management concepts applied to deer. In restrospect, at the time early theory and "principles" were developed, knowledge about deer populations was limited. Technology for monitoring deer populations included binoculars, spotting scope, and horse or motor vehicle. As a result, early observers concluded that deer could not be counted accurately and placed little emphasis on monitoring population characteristics and dynamics in most areas.

Early deer science embraced only limited understanding of the complexities of natural ecological systems and deer-habitat relationships. The knowledge accumulated was based on interactions that were most apparent or discernible within existing technology and management objectives. Improved understanding came later as new

concerns and technology paved the way for more intricate studies of wildlife populations, their environments, and animal-habitat interactions.

Pioneering studies in the western United States were focused on mountain-foothill habitats where mule deer had become abundant and predators were relatively scarce. Deer congregated at high densities on limited winter ranges where an apparent direct correlation between deer numbers, winter forage supply, and over-winter mortality provided a clearly focused management problem. In Montana and other states, biologists extended this interpretation to essentially all environments occupied by both species of deer.

In Montana, game biologists understood carrying capacity as the number of deer a local area could sustain without long-term damage to browse plants supporting the population during winter. The concept of deer habitat primarily considered only the winter forage supply, and it was believed that browsing pressure by deer was the main factor that influenced forage condition and productivity of browse plants. Changes in the browse supply detected through monitoring were believed to reflect changes in condition and productivity of deer populations. The primary techniques employed in deer management were estimates of use and condition of important browse plants, harvest surveys, and indices of fawn survival. Fawn:female ratios lower than 100:100 were considered indicative of deteriorating forage conditions on winter ranges.

Deer populations were presumed to be inherently eruptive, and if unharvested they would increase until they exceeded range carrying capacity and overused the browse supply. Overuse of the browse supply resulted in long-term declines in range carrying capacity and deer numbers. As populations numerically expanded toward carrying capacity, fawn recruitment declined and age structure of the population became older. Consequently, the uniform goal of deer management in Montana emphasized the use of hunter harvest to bring deer numbers into balance with forage supplies (Mussehl and Howell 1970).

This management theory assumed that each incremental decrease in deer density below carrying capacity would result in corresponding incremental increases in fawn production and recruitment (Cole 1961). Increased recruitment resulted from improved quantity and quality of food available to surviving individuals. Such a density-dependent response is often called compensatory reproduction. It was thought to reach an optimum at a population density approximately half the number of deer occurring at "K" carrying capacity. Harvesting the population to this theoretical level each year would result in "Maximum Sustained Yield" (MSY) (McCullough 1984) which represented the maximum number of deer that may be harvested while maintaining a stable population.

Other related principles evolved including compensatory mortality. That is, "In a resilient population, severe loss rates [from many mortality factors] may in effect substitute for each other without mounting up excessively high in total. . . .The death of one individual may mean little more than improving the chances for living of another one." (Errington 1943). This implied that hunting mortality substituted for natural losses

on nearly a 1:1 basis. A deer population experiencing increasing rates of hunting mortality would experience corresponding decreases in natural mortality from starvation.

These relationships are embodied in what is technically called the "density-dependent logistic model." Obviously, most biologists don't inform the public that management decisions are based on such a technical-sounding concept nor that its application involves many assumptions that may not be met in all areas under all environmental conditions. However, this conceptual view guided deer management in Montana for more than 40 years. It subtly gave biologists and the public the false perception that deer populations functioned in a dependable, almost mechanical manner.

Until the 1970s, application of these concepts was logical and convenient because it was assumed that few data were required to assess deer population status. Population trend, fawn recruitment, and adult survival did not need to be monitored. By manipulating hunter harvest, monitoring browse supplies, and occasionally gauging success by monitoring fawn:doe ratios, managers believed the equilibrium between deer and vegetation could be adjusted to increase yield.

For this conceptual view to be applicable, certain assumptions must be made concerning the deer population and its habitat. A logistic population occupies a steady-state environment that provides resources at a constant rate where each individual deer consistently decreased the availability of food for other members of the population. Therefore, changes

in this system were dictated by only a few influential components such as deer numbers and food. Biologists assumed that a population would readily return to a previous state of equilibrium once a perturbing force such as a hunter harvest was removed.

The theories underlying these concepts were developed to mathematically explain growth of laboratory populations of bacteria and insects that grew at a constant rate and reached carrying capacity in very simple closed systems. As implied by Botkin (1990), this theoretical and experimental approach removes the very essence of ecological systems which exhibit variation at all levels of organization and function.

Botkin (1990) concluded that it is impossible to overestimate the influence of these theories on twentieth century population biology. Watt (1962) noted that ecologists believed that their science lacked theory when, in fact, it had too much theory, often borrowed from other sciences, and not carefully connected to field observations. Often, theory and conceptual models are not considered important to the practicing deer biologist. However, as described in previous pages, theory has played a dominant role in shaping traditional concepts of deer populations and their habitats. We can improve the theory and art of deer management if they are implemented in the context of an experimental design (Romesburg 1981, Walters 1986). With these management experiments, we can continually contribute to knowledge about the dynamics of deer populations across the ecological spectrum in Montana.

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An Ecological Perspective

Our profession has traditionally approached management of deer populations and their habitats based on concepts that minimized the importance of variation in all aspects of the system. Management, however, must function within the realm of ecological variation to be successful. Here we present a conceptual framework that explains the dynamics of deer populations within the context of the environmental variation that occurs across Montana.

Our attempts to explain fluctuations in abundance of mule deer and white-tailed deer required an expansion of the concept of habitat to include more than food, cover, and water upon which most traditional interpretations were based. Deer populations function within complex ecosystems. The interface between topography and local climate results in a mosaic of vegetation communities and

a characteristic faunal array along with the distribution of human land uses. All this creates the arrangement of habitats that satisfy the different requirements of the two species of deer. Therefore, the spectrum of deer densities among Montana environments is determined by ecological factors largely beyond the control of management. We observed high deer density where resources for fawn-rearing were of high quality, plentiful, and in close proximity to large areas that optimized deer survival over winter. Low density occurred where resources supporting reproduction and/or survival were scarce or widely distributed.

Superimposed over these landscape level differences were other more localized environmental factors that varied on a daily, seasonal, and annual basis. Fluctuations in the environment resulted in dynamic, short-term changes in conditions favorable and unfavorable for deer (Mautz 1978).

Variation in precipitation and temperature prior to and during the growing season determined forage quantity and quality. Consequently, the physical condition of deer as they entered winter varied from year to year as did winter severity. This relationship between environmental variation and the physiological response by deer can be visualized in terms of an energy balance that has positive and negative periods. During positive periods, energy in the form of high quality forage is plentiful and cost of obtaining it is minimal. The physiological demands of reproduction and recovery of body condition are not only met, but ultimately more energy is

acquired than expended and the excess is "stored" as fat reserves. During negative periods, energy is obtained in the form of poor quality forage which may be scarce and is obtained at high cost. Less energy is taken in than expended, and fat reserves are depleted by basic activities related to survival. Energetics varied between species, among sex and age classes, and from one environment to another. Annual changes in the energy budget experienced by specific deer populations were influenced by variation in these environmental factors and by social interactions that relegated some members of the population to lower quality maintenance habitats. Caughley and Gunn (1993) also concluded that herbivore nutritional status could change independently of herbivore numbers or density in environments with high annual weather variations.

Across many of the environments occupied by deer in Montana, annual variation in precipitation, duration of the growing season, and changes in winter severity would violate an important assumption of the logistic model requiring a steady-state environment. Caughley (1987) indicated that concepts pertaining to ecological carrying capacity were largely an abstraction in environments that experienced substantial variation in annual rainfall. At a minimum, assessment of variation in northern environments must include factors influencing both summer growing seasons and winter severity. These two variables are instrumental in defining the periods of energy surplus and deficit experienced by deer. We contend that variation in many of the environments occupied by deer is of much greater importance to understanding their population dynamics than previously believed. Caughley (1987) concluded that environmental variability "can no longer be ignored as noise, it is now the signal."

In Montana, most environments are not stable, and deer are not equal in their resource requirements. Deer respond to their local environments as individuals. Each has its own unique strategy of habitat use depending on

sex, age, reproductive status, and social position. Behavioral adaptations such as sexual segregation, home range fidelity, and female territoriality during fawning insulate individual deer from direct competition for forage with other members of the population. Social behavior serves as a mediating influence between deer and their environment.

Rather than the traditional view of a balance between a few components (such as deer density and forage quantity), we hypothesize that deer populations vary in accordance with a balance of the total environment (Hamlin and Mackie 1989). Over time, favorable conditions that result in population growth are balanced by unfavorable conditions that result in decline. Environmental variation is measurable, and population fluctuations usually remain within bounds which are characteristic of a particular environment. If the environment fluctuates too widely or changes its character, populations may disappear on a local scale. This has and will continue to happen.

Viable deer populations exist in some places and not in others, and density varies across the species' distribution. The dynamics of deer populations constantly adjust as the environment fluctuates within predictable bounds whether it's the wide swing in variation in fawn recruitment and population size experienced in the prairie-badlands or the narrow swing that occurs in the Salish Mountains of northwest Montana. The outcome is a characteristic set of population parameters that reflect the environmental variation.

Deer Population Dynamics and Hunter Harvest

Deer managers cannot avoid the process of obtaining vital population parameters (fawn recruitment rate, natural mortality rate of adult males and females) as well as monitoring population

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size if the management goal is to optimize harvest. Interaction between fawn recruitment (population gain) and natural mortality of adults (all non-hunting losses to the population) determines the "window of opportunity" for hunter harvest. The effect of a harvest rate on population trend will depend on year to year interactions among these parameters. Also, harvest rate is influenced by weather conditions that affect animal vulnerability and by social changes in hunting pressure and hunter distribution. Our challenge is to monitor biological and social parameters that define opportunity for a corresponding harvest rate that can direct the population toward a defined management goal.

For most populations, annual fluctuations in recruitment rate were much more influential on harvest opportunity than fluctuations in natural mortality rates of adults. Recruitment rates for mule deer were generally lower and more variable than those of white-tailed deer, but recruitment varied across the diverse environments in Montana. In most areas, environmental variation and its effect on energetics determine fawn recruitment to a greater extent than density of deer. Fawn recruitment was dependably influenced by deer density in only the most stable environments augmented by irrigated agriculture.

Average annual rates of natural mortality (malnutrition, predation, disease, accidents, etc.) of adult female mule deer were low and similar (5-7 percent) among the study areas (Table 5). In variable environments, unfavorable conditions can temporarily increase these rates 3- to 4-fold or more. High mortality of adult female mule deer often occurs with the same environmental conditions contributing to low fawn recruitment. Natural mortality rates of female white-tailed deer (≥2 years) varied between 5 and 16 percent among environments (Table 6).

Average annual rates of natural mortality of adult bucks of both species also were quite low (4-9 percent) but increased 5- to 6-fold under certain conditions (Table 7). However, many

adult bucks are shot before they attain an age when they are most vulnerable to natural mortality. Bucks experienced high annual average harvest rates (33-58 percent) in all populations studied. Preliminary results from recent studies in the Bridger Mountains indicate that the annual natural mortality rate of adult mule deer bucks can approach 20 percent in lightly hunted buck populations (Pac and Ross 1993, Pac *et al.* 1995).

A complicated interplay occurs between different types of natural mortality that unfold in a deer population during critically important environmental stress periods. For example, drought during a growing season followed by a long, severe winter often results in several factors impacting deer populations simultaneously. Deer experience a decline in physical condition because of a shorter period of energy surplus and a prolonged period of energy deficit. Small mammal populations often plummet to low levels during drought conditions because of poor vegetation production. Scarcity of mice, voles, and rabbits generally cause coyote predation to shift toward deer.

For most populations, annual fluctuations in recruitment rate were much more influential on harvest opportunity than fluctuations in natural mortality rates of adults.

Predation loss in a deer population has been traditionally considered a compensatory form of mortality. As inferred previously, this means that predation would substitute for other types of natural mortality, and therefore it does not result in further decline in population size. These conclusions were based on the assumption that predators kill only the weak, sick, and old that are part of the "doomed surplus." However, recent studies (Gasaway *et al.* 1983, Hamlin and Mackie 1989, Pac and Ross 1993, and Kunkel 1997) demonstrate that predators such as mountain lions, coyotes, and wolves can also kill healthy, prime-aged ungulates that are unlikely to succumb to other forms of natural mortality in the short term. These predation losses are likely to be additive to other forms of mortality. Therefore, the potential for mortality to be additive varies among different sex and age classes of deer and across a spectrum of environmental conditions. Fawn losses to predators during severe winters would more likely be compensatory because the probability is high that many fawns are in poor condition and may subsequently die of malnutrition (White *et al.* 1987).

However, predators are capable of killing fawns regardless of their physical condition. When high predation loss in summer is followed by continuing high losses to predation and malnutrition during winter and spring, numbers of surviving fawns will be insufficient to replace adult losses.

The effects of predation on deer population size can only be understood in the ecological context of other important factors that influence populations. These factors include annual and seasonal weather patterns that affect relative suitability of important habitats, forage production, forage quality, winter severity, deer physical condition, type and abundance of alternate prey, type and abundance of predators, rates of other types of mortality, and relative size of the deer population.

Some authors conclude that in areas where deer and predators coexist, the ratio between number of effective predators and the number of deer in the population is crucial in determining the degree to which predators may exert an effect on the deer population (Connelly 1978, Keith 1983, Mech 1984, Kunkel 1997).

The effects of predation on deer population size can only be understood in the ecological context of other important factors that influence populations.

In an excellent study on predator-prey relationships, Gasaway *et al.* (1983) cautioned against traditional interpretations of a balance between vegetation and ungulates where the system includes effective predators: "Managers should not use survival of young ungulates as an indicator of the vegetation-ungulate relationship because predation on young obscures this relationship." In this and other studies (Mech and Karns 1977, Hamlin and Mackie 1989, Ballard *et al.* 1991, Boertje *et al.* 1996), predation perpetuated population declines that were initiated by other factors causing ungulates to reach or remain at low densities even after a return of favorable environmental conditions.

Our results also indicated that reducing population density through hunter harvest will not dependably stimulate higher rates of fawn recruitment. As previously discussed, this is most apparent in variable environments where deer experienced drought and winter energy deficits and coexisted with effective deer predators. However, in riverbottom-agricultural environments, hunter harvest can stimulate socially-based, density-dependent increases in fawn recruitment where populations exist on a high nutritional plane yearlong and coexist with low numbers of effective deer predators.

Biologists traditionally believed that deer killed by hunters would substitute for deer that would otherwise die of natural causes. In practice, traditional theory implied that substitution operated on nearly a 1:1 basis because of intense competition for limited food on winter ranges. Obviously, some proportion of hunting mortality will replace natural mortality. The question is how much? Our results indicated that opportunity for substituting hunting mortality for natural mortality varies among species, populations, and sex and age classes. In most deer populations, hunter harvest of fawns has the highest probability of substituting for mortality experienced over winter because fawns experience higher natural losses than adults during

that time of year. Harvest of adult does has a comparatively lower probability of substitution because young and prime-aged females experience very low rates of natural mortality (Hamlin and Mackie 1991, Dusek *et al.* 1992). Consequently, harvest of prime-aged females would more likely be additive to natural losses.

The rate of adult female natural mortality in harvested populations did not decline with significant increases in harvest rate. In other words, adult female harvest during autumn did not increase survival of remaining adult females during the subsequent winter. This relationship is graphically portrayed in Fig. 61A for mule deer does in the Missouri River Breaks. The low and narrow span of natural mortality rates of adult does occurred across a wide spectrum of hunter harvest rates ranging from near zero to 30 percent. Therefore, it is not surprising that annual survival rates of adult females declined in a linear relationship as hunting mortality rate increased in this population (Fig. 61B). However, the influence of any change in female survival rate on population trend depended on the recruitment rate of incoming one-year-old females.

The proportion of hunting mortality of adult females that is compensatory (substitutes for other losses) would have little impact on population trend. In contrast, the additive component of the harvest has the potential to influence trends in population size. This potential can only be evaluated in relation to rates of natural mortality and fawn recruitment in the population at the same time. For example, even though a substantial proportion of adult female harvest may be additive to other mortality, a population will not decline if fawn recruitment is adequate to replace the combined losses. Under conditions of very low fawn recruitment, any hunting mortality of adult females in combination with other losses could initiate or intensify a population decline.

The buck segment of most deer populations is harvested at rates up to 10 times greater than adult females (Tables 6 and 7). We did not observe high rates

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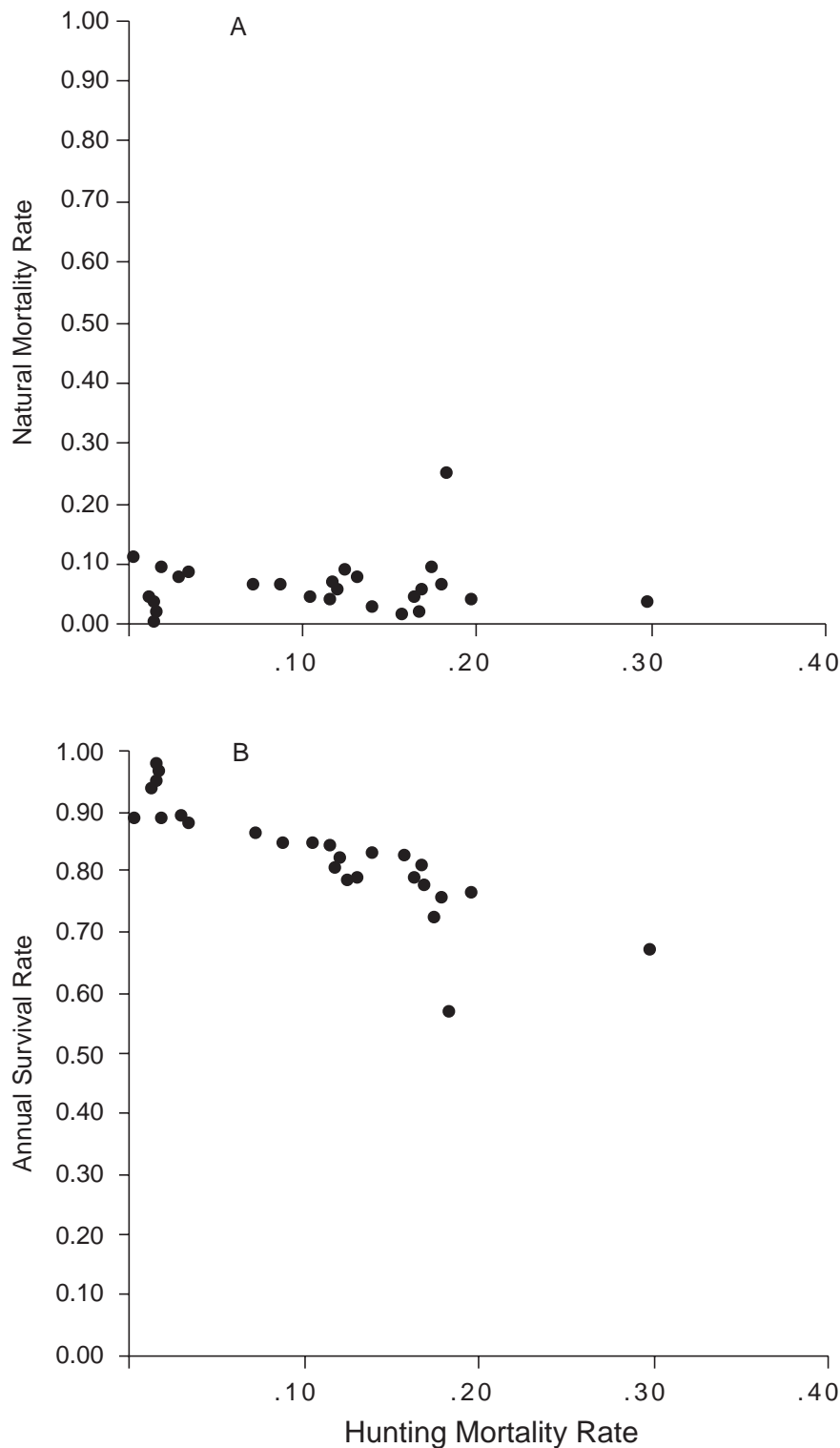
*Figure 61.
Relationships
between annual
natural mortality
rate and annual
hunting mortality
of adult female
mule deer (A) and
annual survival
rate and annual
hunting mortality
rate of adult female
mule deer (B) in
the Missouri Breaks
(after Hamlin and
Mackie 1989).*

of natural mortality among bucks in the populations we studied because high harvest rates precluded opportunity for most adult males to die of natural causes. In the absence of substantial harvests, however, adult bucks may experience

higher natural mortality rates than adult females. Pac *et al.* (1991) and Pac and Ross (1993) reported that predation loss was apparently higher among all age classes of bucks. Also, bucks became vulnerable to winter mortality at an

earlier age than females. Consequently, compared to those rates listed in Table 7 for heavily exploited buck populations, natural mortality rates of adult bucks would likely increase under special buck management strategies that expand age diversity.

Montana deer populations contain fewer bucks than does. Therefore, recruitment of equal numbers of male and female fawns adds proportionately greater numbers to the male segment. This means that the male segment can remain numerically stable while experiencing a higher mortality rate than adult females. The degree to which males can be harvested more heavily than females depends on the fawn recruitment rate and the post-season male:female ratio the deer manager would like to maintain. Fawn recruitment and adult mortality rates are not stable, and averages are seldom applicable in variable environments. However, it is important to understand how variation in fawn recruitment and adult mortality can influence trends in availability of the two sexes.

Relationships between recruitment and adult mortality are modeled in Fig. 62. The importance of these relationships is not in their absolute precision, but in providing insight to the probable outcome of harvest rates relative to recruitment in a particular year. Values of recruitment and mortality that intersect to the left of the female curve (Fig. 62A) correspond to increases in the female population. Values to the right of the female curve initiate a decline. For example, if 40 fawns:100 females are recruited and total mortality of adult females from all causes exceeds 17 percent, numbers of adult females will decline. In most Montana mule and white-tailed deer populations, recruitment is almost never high enough to maintain stability in the female segment when total adult female mortality, including harvest, exceeds 33 percent.

At 30 fawns:100 females recruited in spring, a sex ratio of about 15 bucks:100 does can be maintained when annual buck mortality is about 50 percent (Fig. 62B). At the same recruitment rate, a buck:doe ratio of 40:100 could be maintained if buck mortality was reduced to about 30 percent. This graph is most applicable to populations experiencing low adult female harvest rates or stable female populations because buck:doe ratios are influenced by relative differences in rate of harvest of the sexes. Also, relationships in the graphs are based on the assumption that density dependence and compensation are not significant influences on fawn recruitment and adult mortality.
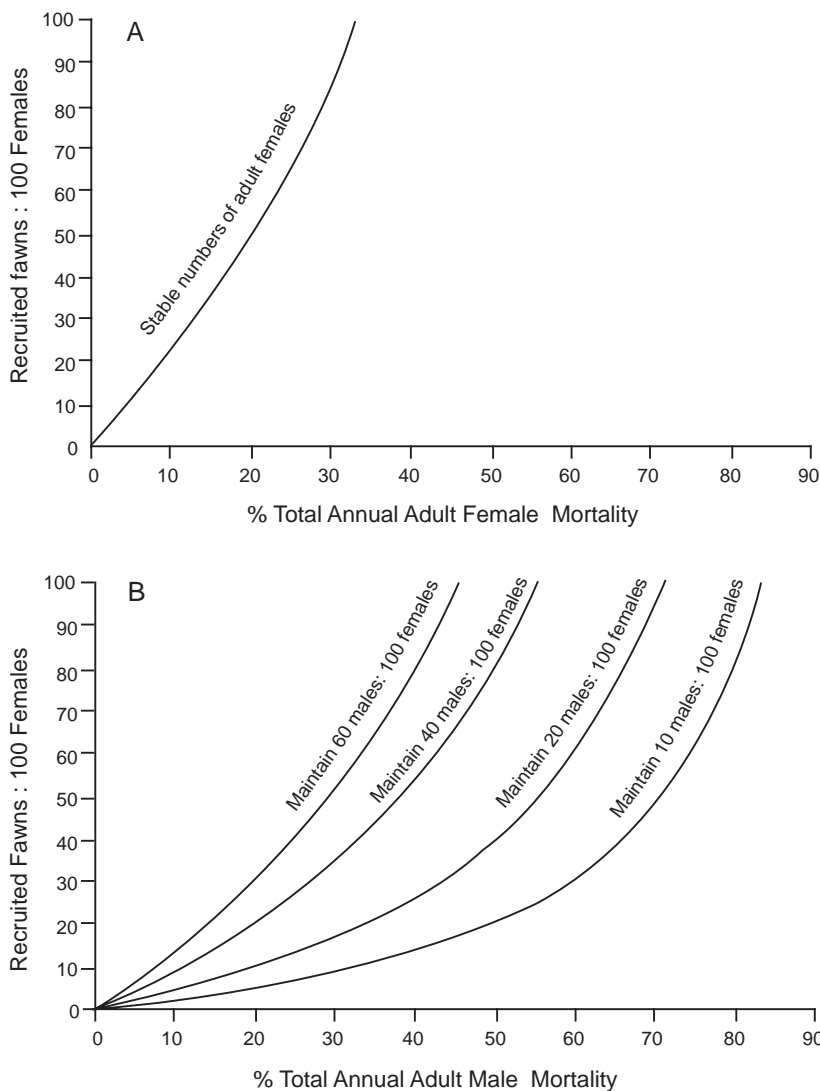
Figure 62.
Relationships between fawn recruitment and total annual mortality of adult females that maintain stable numbers of does in the population (A) and fawn recruitment and total annual mortality of adult males that maintain stable buck:doe ratios in the population (B) (after Hamlin and Mackie 1989).

Deer Management in Specific Ecosystems

All wildlife populations are products of the land, inextricably tied to the habitat that supports them (Leopold 1933). Mule deer and white-tailed deer fill different niches, even locally. Mule deer tend to occupy rugged, broken topography with more variable climatic conditions, and white-tailed deer tend to occupy more gentle topography. East of the Continental Divide, whitetails are often associated with riparian communities and agricultural croplands. West of the Continental Divide, white-tailed deer occur in association with riparian components of coniferous forests.

We realize that the environmental settings occupied by deer are endlessly variable, and any attempt to categorize them will include numerous deficiencies. Nonetheless, we believe the potential benefits of aligning deer management goals and strategies with differences in population dynamics across the ecological spectrum will outweigh potential problems (Table 8). Biologists can fit

Table 8.
Major environment types occupied by mule deer and white-tailed deer in Montana.

Mountain Ecosystem
    Mountain-foothill Environment
    Northwest Montane Forest Environment

Prairie Ecosystem
    Timbered Breaks Environment
    Prairie-Badlands Environment
    Prairie-Agricultural Environment

Riverbottom Agricultural Ecosystem
    Plains Riverbottom Environment
    Intermountain Valley Environment

specific deer populations into the general management categories we describe in subsequent sections.

Deer population response to fluctuation in different environments is portrayed in pendulum graphs in the following section (Figs. 63-66) . In Montana deer periodically experience unfavorable conditions that correspond to a long energy deficit (severe winter) and short energy surplus (poor growing season). This results in declining physical condition of deer and increases in predation and winter mortality. Under these conditions populations enter a low output phase characterized by minimal fawn recruitment and relatively high natural losses of adults. During this phase opportunity for hunter harvest is limited unless reduction in population size is desired.

Short periods of energy deficits and long periods of energy surplus result in improved physical condition. With this the population enters a high output phase characterized by high fawn recruitment and low natural mortality of adults. Higher rates of hunter harvest are then required to stabilize population size.

We assimilated information from Tables 4-6 and Fig. 62 to describe interrelationships between fawn recruitment, adult female natural mortality, hunter harvest of does, and their combined effect on adult female population trend. The amplitude of the pendulum swing (Figs. 63-66) represents the outer limits of expected variation in these parameters as the population responds to fluctuations in a given environment. The solid pendulum bars

delimit the ave. ± 1 std. deviation in population parameters while the dashed pendulum bars represent highest and lowest recorded values. Adult female harvest rates indicated at each level of output would stabilize numerical growth in the female population. The graphs provide general guidelines for selecting adult female harvest rates that may direct populations in various ecosystems and environments toward desired management goals.

Mountain Ecosystem

The mountain ecosystem contains populations of both species of deer that collectively occupy most of the western third of Montana including essentially all of MFWP Regions 1, 2, and 3, and mountain ranges in Regions 4, 5, and 6 (Fig. 1).

Mule deer predominate in drier mountain-foothill environments such as the Garnet Mountains west of the Continental Divide and most mountain ranges east of the Divide. Mule deer are also found in the higher elevation portions of mountain ranges in the northwest montane forest environment.

White-tailed deer predominate in densely-timbered river valleys and maritime-influenced mountain ranges in western and northwestern Montana. Examples include the Salish Mountains, and the mountains and valley bottoms associated with the Swan, Fisher, and Blackfoot Rivers.

White-tailed deer also are locally abundant in foothills and along drainages into some mountain ranges east of the Continental Divide where deer have access to agriculture on a seasonal or yearlong basis. Examples include the Big and Little Snowy Mountains, Bears Paw Mountains, Rosebud Plateau, and portions of the Moccasin and Judith Mountains. However, little is known about the population dynamics of white-tailed deer in this ecological setting. Additional investigations are needed to adequately describe population parameters and harvest relationships of whitetails in the mountain-foothill environment east of the Divide.

Description of Deer Population Ecology

Both species congregate on their respective winter maintenance habitats in the lower foothills and river valleys where deer occur at densities of 6-60 deer/km^2. In summer, deer exploit both adjacent and distantly located reproductive habitats at higher elevations where densities vary from 1-15 deer/km^2.

In mountainous terrain, both species of deer contend with an energy deficit during winter that is often of longer duration than experienced by deer in other environments. During winter, the primary survival strategy emphasizes specialized use of habitat to conserve fat reserves. Duration and severity of the deficit varies from year to year. It can also vary locally depending on elevation and relief of the local landform and climate, especially the relative tendency to accumulate snow. East of the Continental Divide, some mountain ranges occupied by mule deer occur in the "chinook zone" where snow cover periodically melts during the winter

months. Other mountain ranges outside this zone retain their low-elevation snowpack throughout the late autumn-spring period.

Delayed snowmelt and plant growth are typical of some mountain areas where high elevation ranges comprise much of the summer habitat. In these situations, mule deer populations experience "bottlenecks" in seasonal distribution. Compared to lower elevation mountain ranges, deer exploiting high elevations spend more time confined to winter range and as much as 70 fewer days on their summer home ranges (Pac *et al.* 1991). White-tailed deer occupying the maritime influenced mountain ranges in northwest Montana usually experience less variation in precipitation and temperature during summer and winter.

In all types of mountain environments in Montana, deer must recover physical condition, reproduce, and accumulate fat reserves for the coming winter during a comparatively short summer growing season. To be successful, most deer in mountain environments employ specialized migratory movements that are passed from one generation to the next by social bonds within matrilineal groups.

The relationship between habitat and deer abundance is far more complex in mountain environments than previously understood. Specialized behavioral responses to severe environmental conditions contrasted with the traditional concept of predicting deer numbers simply from the amount of forage available in winter. We also were unable to document a relationship between adult density and fawn recruitment (Mackie *et al.* 1990, Pac *et al.* 1991). While critical to the occurrence of deer in mountain environments, winter range was not the primary factor determining deer numbers and dynamics.

In mountainous terrain, both species of deer contend with an energy deficit during winter that is often of longer duration than experienced by deer in other environments.

In most mountain ecosystems, deer persist under the potential influence of several effective deer predators. These commonly include coyotes, mountain lions, black bears, and bobcats. A few mountain environments also include grizzly bear and/or recolonizing wolf populations.

Each of these predators tends to exploit prey in a characteristic manner and each is most effective in a particular environmental setting. The mountain lion and wolf occur at relatively low abundance and are capable of killing any sex or age class of deer regardless of size or condition (Kunkel 1997). Comparatively coyotes may occur in higher densities in some mountain environments. However, coyotes are more opportunistic feeders such that predation on deer may vary substantially and unpredictably from year to year. Less is known about the potential impacts of black bears and bobcats on deer. They were not significant in killing mule deer older than six months of age in the Bridger Mountains (Pac and Ross 1993). Their effectiveness at killing deer fawns between birth and 6 months of age has not been studied in mountain environments. However, black bear have been documented as substantial predators of newborn elk calves in mountain environments (Schlegel 1976).

The combined effects of multiple predators could exert greater and more consistent predation pressure compared to other environments with fewer effective deer predators.

Potential exists for predation to influence population trend in the mountains of western Montana. The combined effects of multiple predators could exert greater and more consistent predation pressure (MacNab 1985) compared to other environments with fewer effective deer predators. In the North Fork of the Flathead River, Kunkel (1997) indicated that the white-tailed deer population was declining because of low fawn recruitment caused by the additive effects of multiple predators.

White-tailed deer populations in northwest Montana increased to an apparent record high level during the last 20 years. This probably resulted from favorable habitat changes, mild winters, low hunter harvest rates, and possibly a numerical advantage favoring deer in the presence of predators. However, the increasing trend could end in the face of a catastrophic winter. If adult female harvest rates were high in conjunction with high predation and poor fawn recruitment, a significantly lower population could persist for a time even after a return to favorable environmental conditions.

Mule Deer Vital Parameters and Harvest Recommendations —Mule deer fawn recruitment rates (ave. = 33 ± 13 fawns:100 females) in mountain-foothill environments are low compared to populations occupying other ecosystems (Table 4). Somewhat higher recruitment rates may be observed in some mountain ranges where the period of energy deficit is shorter or deer have seasonal access to agricultural crops. However, recruitment rates from the Bridger Mountains incorporated estimates of fawn mortality through mid-May. On other areas, classification data often miss significant pulses of fawn mortality that periodically occur after March.

Natural mortality rate of adult females (7 ± 6 percent, Table 5) was similar to that of mule deer in timbered upland breaks or prairie-badlands. The interaction of fawn recruitment and natural mortality of adult females presents a rather narrow opportunity for hunter harvest of adult females (Fig. 63). The low output phase corresponded to recruitment rates ≤ 20 fawns:100 females and natural mortality rates ≥ 14 percent among females. A goal of maintaining reasonable stability in the doe population leaves little opportunity to harvest adult females during lower output phases. Harvest opportunity is restricted because of the low number of incoming recruits. If the goal is to reduce the population, however, the low output phase is an excellent time to harvest adult does.

When the population enters a high output phase during favorable environmental conditions, female harvest rates of 15-21 percent are required to keep it from increasing. This corresponds to recruitment of ≥ 45 fawns:100 females and natural losses of does ≤ 3 percent. The population
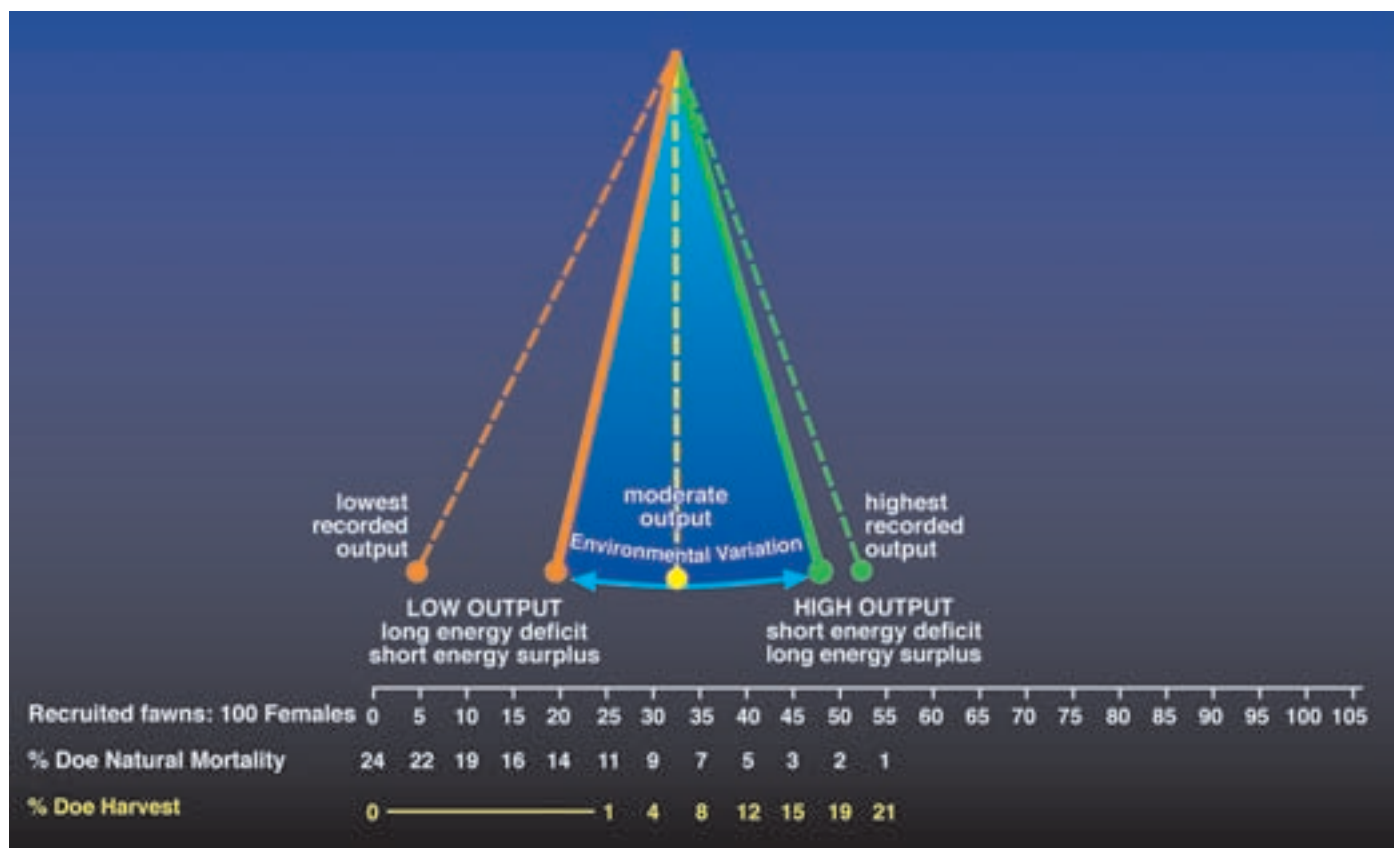
Figure 63.
Recommended mule deer doe harvest rates across the span of expected variation in fawn recruitment and
natural mortality of adult females in a mountain-foothill environment.

varies across a span of moderate output during about 6 of every 10 years. During these years, it can support a doe harvest of 1-15 percent. However, mule deer populations can exhibit considerable variation in the length of time they remain within a particular output phase. Also, other situations can occur where fawn recruitment and adult female mortality rates on the pendulum graph do not align with each other.

Special Mule Deer Population Management Issues—In recent years, public controversy concerning mule deer management has centered in the mountain-foothills where hunting is focused on public lands. Two issues are of primary importance.

First, the public demands improved detection of population declines and expects a more timely harvest management response. This will require improved population monitoring and a more integrated process for implementing appropriate regulations in response to significant changes in population status. The margin of error is small in managing female mule deer harvest on vast expanses of accessible public land where high numbers of elk hunters result in increased hunting pressure on deer (Hamlin and Erickson 1996). Conservative harvests should be applied to these areas where female harvest is not required to solve game damage problems. A large population of productive females is required to maximize buck fawn yield to sustain the heavy buck harvest rates that prevail in these settings. Recolonization will occur slowly in areas that have been heavily harvested because recruitment and emigration rates are low. This problem becomes critical when it involves population segments with specialized

...the public demands improved detection of population declines and expects a more timely harvest management response.

migratory movements to distantly located summer ranges (Kasworm 1981, Pac *et al.* 1988). Management effectiveness will be enhanced if hunting district boundaries are aligned to the ecological boundaries of individual populations.

Second, creative strategies are needed to improve hunter opportunity to harvest older, larger-antlered mule deer bucks. Many mule deer populations in Regions 2 and 3 have few bucks older than 3 years. Any buck management strategy that strives to increase age diversity will require reducing annual hunting mortality from the prevailing 50-70 percent to about 35 percent or less. This will probably require a substantial reduction in the number of hunters afield. To produce bucks with large antlers, the age structure must include bucks ≥4 years. However, natural mortality rates rise with age and bucks seldom survive beyond their seventh year.

Some habitats may provide greater opportunity than others for sustaining older mule deer bucks. Thus, increasing the availability of mature bucks will be most efficient when directed at specific populations or hunting units. Further discussion of buck population trends and review of some management strategies is provided in the Draft Environmental Analysis for establishing the 1997 Deer Hunting Season (Hamlin and Erickson 1996). Buck:doe ratios and antler characteristics by age class in different environments are also discussed in that document.

White-tailed Deer Vital Parameters and Preliminary Harvest Recommendations —The northwest Montana white-tailed deer project is ongoing, and data have not been completely analyzed in a manner allowing construction of a pendulum graph. Nonetheless, data are available to make preliminary harvest recommendations. Sime (1996) reported that the white-tailed deer fawn recruitment rate in the Salish Mountains (ave. = 67 ± 18 fawns:100 females, Table 4) was higher than the recruitment rate for mule deer in mountain-foothill environments.

In northwest montane forest environments, the natural (non-hunting) mortality rate of whitetail does is 0.10 (95 percent C.I. 0.07 - 0.13) (Sime unpubl.). This estimate represents a cumulative rate using the analysis technique MICROMORT (Heisey and Fuller 1985) for all radio-collared females monitored between 1988 and 1995.

Similar to the relationships shown for other populations, white-tailed deer in northwest montane environments probably fluctuate between low, moderate, and high output phases. To make harvest recommendations prior to a thorough analysis of research data, we suggest that the cumulative natural mortality rate of 10 percent could be interpreted as the natural mortality rate when the population is in a moderate output phase. The 95 percent confidence interval would probably represent upper and lower bounds of variation in natural mortality while the population is operating in high or low output phases.

When northwest montane white-tailed deer populations are in the moderate output phase, defined by a recruitment rate of 67 fawns:100 females and a natural mortality of 10 percent, a 15 percent harvest rate of adult females would be necessary to prevent increases in numbers of females. During the high output phase with recruitment of 85 fawns:100 females and 7 percent natural mortality, a 23 percent adult female harvest rate would prevent population growth. When populations are in the low output phase with recruitment of 49 fawns:100 females and 13 percent natural mortality, a 7 percent harvest rate of adult females would be sufficient to prevent population growth.

Annual mortality of whitetail bucks on the Salish Mountains study area averaged 42 percent compared to 61 percent in a prairie-agricultural environment (Table 7). In the northwest montane forest, annual mortality attributed to hunting averaged 33 percent and natural mortality accounted for 9 percent. Relationships portrayed in Fig. 62 indicated that buck:doe ratios approaching 50:100 could be maintained

Management effectiveness will be enhanced if hunting district bondaries are aligned to the ecological boundaries of individual populations.

when recruitment averaged about 65 fawns:100 females.

The severe winter of 1996-97 represents the lowest recruitment rate ever observed for this population. At the time of measurement in March 1997, the recruitment rate was 30 fawns:100 females. However, actual recruitment likely fell below that value because deer were confined to winter ranges for another two months. Migrant deer did not begin leaving the winter range until mid-May and some stayed until late May. Incidental observations gathered in April and May indicated that the fawn:adult ratio continued to decline.

Because of the severity and duration of the 1996-97 winter, a separate accounting of adult female natural mortality was made between the close of the general hunting season December 2, 1996, and June 1, 1997, for those females marked previously and whose radio collars were still functioning June 1. In that 6 month interval, 26 percent of the radio-collared adult females died. On an annual basis, natural mortality during 1996-97 must have exceeded 26 percent and was probably at least 31 percent, assuming that at least 5 percent died during the remainder of the year.

When recruitment falls to 30 fawns:100 females or less and adult female natural mortality is 26 percent or greater, all adult female harvest is precluded if the management goal is to maintain the population at the current level. Given these values, the population is already in decline, regardless of the antlerless harvest rate, because natural mortality exceeds recruitment.

At the opposite end of the spectrum, some years appear to have been very favorable for whitetail populations in northwest montane forest environments. The highest observed recruitment rate was 96 fawns:100 females. In the best of years, adult female natural mortality could reasonably be estimated at 5 percent. This value is similar to other study populations with actual annual mortality estimates for the most favorable years. Under such highly favorable conditions, a 27 percent adult female harvest rate

is necessary to stabilize numbers of adult females in whitetail populations in montane environments.

Habitat Management in Mountain Ecosystems

Management recommendations concerning land use issues will be most effective when they are based on knowledge of yearlong deer habitat use, seasonal distribution, and specific resource requirements of an individual population. Requirements of both species in winter emphasize conservation of fat reserves. White-tailed deer may use agricultural crops where available, and use varies from year to year depending on winter severity (Kamps 1969). Whitetails usually rely on an energy conservation strategy during harsh winters and are more opportunistic during mild winters. In summer, reproductive requirements are met by using a diversity of vegetation communities centered in riparian areas.

Housing Developments—Many western Montana deer habitats occurring on private land have been subdivided, particularly in MFWP Regions 1, 2, and 3. We recommend that biologists be involved as much as possible in city and county planning efforts. Accurate information on location of seasonal ranges, movement patterns, and population size can significantly influence outcomes in the planning process. Cluster development can preserve open space and minimize human disturbance. Conservation easements could be pursued on priority areas under private ownership.

For mule deer winter ranges east of the Continental Divide, housing densities of <2 homes/km^2 caused relatively little conflict between deer and people other than periodic game damage complaints in these rural agricultural settings. At housing densities of 3-8 homes/km^2, the winter range becomes a complicated mix of urban and agricultural land uses. Segments of the local deer population adapt to the new cover and forage sources associated with housing development and become somewhat conditioned to human presence. Deer damage

complaints accelerate, and effective solutions such as sport hunting decline. Deer are considered a nuisance in these situations by some individuals and a resource by others. This creates conflict between neighbors and between housing development residents and the statewide wildlife agency (Baker and Fritsch 1997). Vogel (1989) indicated that densities of >12 homes/km^2 virtually preclude use by deer in an intermountain valley environment.

Timber Management—Timber management on winter maintenance habitat should emphasize retention of conifer forest stands because of their importance when deer habitat use strategies emphasize conservation of energy reserves. Mature conifer forest is often preferred by both species during deep snow conditions and severe weather in the northwest montane forests and some mountain-foothill ranges (Pac *et al.* 1991, Baty 1995). In some areas, availability of conifer cover in winter may be essential to the occurrence of deer. Conifer cover ameliorates temperature extremes, and reduces wind velocity and radiant heat loss. Snow depth under the conifer canopy is also minimized,

providing easier access to foraging sites (Youmans 1979). White-tailed deer consistently preferred overstory canopy coverages > 50 percent and showed no preference for any overstory canopies < 41 percent during severe winter conditions (Baty 1995). During storm-free winter conditions, mule deer preferred open Douglas fir stands often associated with steep shrub fields and rock outcrops that acted as "solar radiators" (Steerey 1979, Youmans 1979).

Our studies and those of Baty (1995), Stansberry (1996), and Baty *et al.* (1996) found no evidence that commercial thinning of conifer canopies or reduction in understory conifer density was desirable on winter ranges where deer frequently contend with deep snow conditions. Baty *et al.* (1996) hypothesized that white-tailed deer population productivity could decrease due to reduced cover and increased energy expenditures and recommended against broadscale silvicultural practices that create open savannah-like stands of mature ponderosa pine on white-tailed deer winter ranges west of the Continental Divide. However, he indicated that such changes my be neutral for mule deer and beneficial for elk. Arno *et al.* (1987) recommended coupling prescribed fire with small partial cutting units (0.1-0.6 ha) to perpetuate the overstory canopy and stimulate forage production on whitetail winter ranges in the northwest montane forest.

Timber management to optimize deer habitat and maintain or increase deer numbers on summer ranges should emphasize perpetuation or enhancement of habitat diversity. For mule deer in mountain-foothill environments, mature (150-300 years) Douglas fir stands provide critical fawn-rearing habitats (Pac *et al.* 1991). These often uneven-aged stands have irregular

canopies and structure that promote a patchwork of understory diversity. High quality forage resources and security for fawn rearing occur in optimal combination in topographically complex forest communities.

For mule deer in mountain ranges east of the Divide, timber management should avoid large scale removal of these stands to ensure that regenerating stands are allowed to reach the age where these attributes are replaced. Cutting units that focus on large, even-aged stands of lodgepole pine could benefit mule deer. Small, irregular shaped cutting units (0.5-2.0 ha) will maximize edge effect and minimize reduction in habitat security when loosely distributed across large stands.

For white-tailed deer occupying northwest montane forests, Morgan (1993) concluded that riparian areas and adjacent uplands containing pole/immature timber were very important as centers of deer use in summer. Many of these habitat complexes were found between 1,100 and 1,700 m in elevation on east to southeast aspects on the Tally Lake Ranger District. Cutting units would have minimal effect on white-tailed deer if located on northerly and westerly aspects, ridgetops, and other sites more than 750 m from riparian habitat.

Road Management—Road building proliferated in many western Montana mountain ranges with the rapid expansion of timber harvest on public and private lands during the last 50 years. Road building represents a two-sided issue for deer management in mountain ranges east and west of the Continental Divide. Access is necessary for even distribution of the deer harvest. However, too much access on public lands contributes significantly to low escapement by bucks during the hunting season. Unfortunately, most road building was conducted without considering security needs of deer during the hunting season. This problem is acute in areas where mule deer and elk distribution overlaps and hunting pressure is high (Hamlin and Erickson 1996).

Road management guidelines must be tailored to specific objectives for managing deer in a particular area. If maximum deer harvest is appropriate, extensive open road networks may be beneficial. Restrictions on use of open roads and limitations on building new roads could be incorporated in strategies for improving or maintaining buck deer age diversity. Otherwise, deer population objectives will continue to be accomplished through significant reductions in hunting opportunity.

Morgan (1993) reported that roads in habitat used by white-tailed deer during summer-early autumn in northwest Montana, did not negatively affect deer distribution and use except immediately adjacent to roads. Closing roads in the most preferred habitats could be beneficial to deer in the immediate vicinity.

Habitat Enhancement and Vegetation Manipulation—During the last 50 years, extensive effort has been directed at vegetation manipulation to increase the amount of forage available on winter ranges in the western United States. Numerous studies show positive responses in ungulate distribution and use related to habitat manipulation (Anderson *et al.* 1974, Riggs and Peek 1980, Bentz and Woodard 1988, Klinger *et al.* 1989). Stansberry (1996) evaluated habitat enhancements on mule deer and bighorn sheep winter range adjacent to and above the area inundated by the formation of Lake Koocanusa in northwest Montana. He concluded that forage production was increased by slashing, burning, and fertilization. Although animal use apparently increased following the treatments, increases of numbers, productivity, and survival of deer or bighorn sheep were not observed. These results generally agreed with other studies (Cook *et al.* 1989, Klinger *et al.* 1989, Stussy 1993). We recommend that deer habitat improvements in mountain environments focus on acquisition or easements that protect the ability of deer to use winter ranges in an undeveloped and undisturbed condition. Land use practices that eliminate important

vegetation communities such as multi-aged stands of conifer forest (Baty *et al.* 1996) or sagebrush/grassland communities (Peterson 1996) can be expected to have negative consequences.

Livestock Grazing—Scientific studies of the relationships between livestock grazing and deer populations have not been conducted in mountain environments in Montana. Specifically, relationships between cattle grazing, small mammal abundance, and coyote predation on mule deer require further study.

Cattle grazing on summer ranges occurred primarily on drainage bottoms and areas of low topographic relief. These areas were often selected by white-tailed deer, resulting in potential for competitive interaction. Spatial overlap with mule deer was limited by their preference for more rugged terrain. However, intense summer-long livestock grazing over large areas of diverse Douglas fir communities also could decrease habitat quality for mule deer.

Prairie Ecosystem

Prairie extends across much of the eastern two thirds of Montana, dominating significant portions of Regions 4 and 5 and the majority of Regions 6 and 7 (Fig. 1). Included in the prairie ecosystem are three distinct environments: timbered breaks, prairie-badlands, and prairie-agricultural. Landforms vary from flat to highly eroded, rugged badlands. The climate is semi-arid and volatile fluctuations occur during all seasons. Vegetation is characterized by grassland, shrub/grassland communities with hardwood draws or other woody cover along some drainages, and pine-dominated dendritic "breaks." Land ownership is predominantly public in the timbered breaks and mostly private in prairie-badland and prairie-agricultural environments. Dryland agriculture and livestock grazing represent the primary economic land uses. As in all parts of

Montana, recreational hunting of deer is an activity of significant economic value.

Mule Deer Population Ecology in Timbered Breaks Environments

Our knowledge base concerning mule deer population ecology in timbered breaks environments (Hamlin and Mackie 1989) may be more complete than for either species in other parts of Montana. Mule deer density on the Missouri River Breaks study area varied between 1.4 and 6.2 deer/km^2 during a 27-year period (Hamlin and Mackie 1989). Elsewhere, higher densities occurred locally where timbered breaks included agriculture. Mule deer density in an upland pine/agricultural area in the lower Stillwater River drainage of southcentral Montana varied from 7-19 deer/km^2 during 1979-97 (Stewart, personal communication 1997).

Individual deer displayed either resident movement patterns or short distance seasonal migrations. Fawn-rearing habitats closely interspersed with small, scattered inclusions of winter habitat served the needs of family groups of resident deer. Seasonal migrants made short distance connections between summer habitat in upper coulees with wintering areas in rough topography at the lower end of coulees.

In the timbered breaks, significant variation in annual precipitation and temperature results in dramatic changes in forage production and the duration of succulence during the growing season. The effects of these environmental factors on forage quantity and quality were much more influential than browsing by deer. An equilibrium relationship (carrying capacity) between deer and forage supplies seldom unfolded in a definable or predictable manner. However, Hamlin and Mackie (1989) indicated that fawn survival to December could be predicted from the same factors that significantly predicted forage quality. These factors were precipitation during July-April prior to the growing season and temperatures during May.

Although weather conditions are highly variable, winter is usually over by mid-March. Length of the winter deficit period is about one month shorter than experienced by mule deer in mountain environments.

The classic logistic relationship between population density and fawn recruitment rate did not predictably operate in this variable environment. During favorable environmental conditions, fawn recruitment could be excellent at high population density. It could also be poor at minimal population density if conditions were unfavorable for fawn survival. Hamlin and Mackie (1989) indicated that mortality rates can be nutrition related but not necessarily related to density of deer in the population.

In timbered breaks, mule deer coexisted with the coyote as the only effective deer predator. Coyote density was apparently higher in the timbered breaks compared to other parts of eastern Montana (Pyrah 1984). Hamlin and Mackie (1989) reported that predation rate on mule deer varied significantly from year to year even though coyote population size was relatively constant.

This occurred because coyotes displayed flexible and opportunistic food habits (Schladweiler 1980). Increases in coyote predation of mule deer often occurred during drought conditions or other periods when small mammal populations were low. Some of the predation loss was additive and significant in its effect, particularly when the deer population was low as a result of a combination of mortality factors.

Mule deer populations in the timbered breaks are capable of quickly rebounding from population lows. Their numbers have doubled in 2 years when environmental conditions were favorable. Lush summer growing seasons, abundant small mammal populations that serve as alternative prey for coyotes, and mild winters contribute to population recovery. Deer numbers can also decline by 50 percent or more in years of unfavorable conditions.

White-tailed deer populations of management importance occur locally where inclusions of river bottom-agricultural or prairie-agricultural environments occur within the timbered breaks. Habitat issues concerning these populations are similar to those discussed

in later sections concerning whitetails in riverbottom-agricultural and prairie-agricultural environments.

Mule Deer Vital Parameters and Harvest Recommendations—Populations in the timbered breaks displayed greater fluctuation compared to populations in the mountains. In the former, recruitment averaged 51±27 fawns:100 adult females compared to 33±13 fawns:100 adult females in the mountains (Table 4). During unfavorable environmental conditions in the timbered breaks, recruitment varied from 5-25 fawns:100 adult females (Fig. 64). A significant pulse of high natural mortality of adult females often, but not always, occurred in concert with low fawn recruitment. The magnitude of this pulse, which varied from 11-24 percent of adult females, could initiate a population decline even in the absence of any measurable female harvest. Opportunity for female harvest is limited during the low output phase unless further reduction in the population is desired.

During most years, the population fluctuated across a wide but moderate output phase indexed by recruitment rates of 30-75 fawns:100 adult females. Natural mortality rates of adult females during this phase are generally low, varying from 1-10 percent. Corresponding adult female harvest rates vary from 3 to 24 percent during the moderate output phase.

At high output, the population experiences recruitment ranging between 75 and 103 fawns:100 adult females. A female harvest of 26-33 percent is required to stabilize adult female numbers.

Emigration is a form of population loss that is hard to document and to incorporate into harvest prescriptions. Emigration of yearling females was

Populations in the timbered breaks displayed greater fluctuations compared to populations in the mountains.
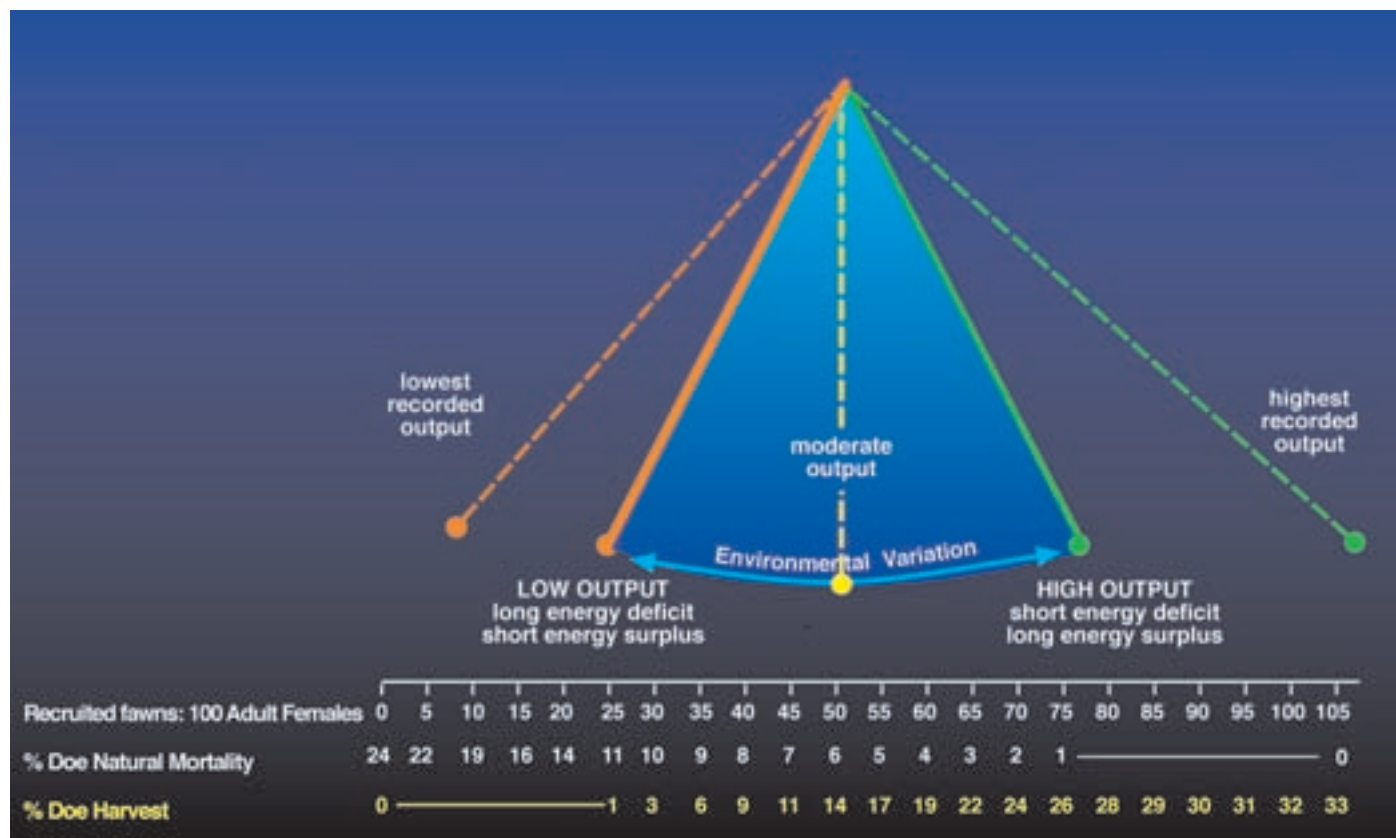
Figure 64.
Recommended mule deer doe harvest rates across the span of expected variation in fawn recruitment and natural mortality of adult females in a timbered breaks environment.

significant and apparently not balanced by immigration at the lowest and highest female densities recorded on the Missouri River Breaks study area (Hamlin and Mackie 1989). Substantial emigration usually occurred among yearling females in the first two large cohorts following a low population phase. It also accounted for about 50 percent of a yearling female cohort recruited during a high population. However, emigration did not increase proportionally with population density. The harvest rates we indicate on the pendulum graph (Fig. 64) would be greater than necessary to stabilize the female segment in core populations during years of high yearling female emigration.

Annual mortality rate of mule deer bucks on the Missouri River Breaks study area averaged 41 percent compared to 46 percent recorded in the Bridger Mountains and 61 percent on Cherry Creek (Table 7). In the timbered breaks environment, annual mortality attributed to hunting averaged 37 percent and natural mortality accounted for the remaining 4 percent. However, hunting mortality rates fluctuated from 15-58 percent and natural mortality rates varied from 0-11 percent among individual years. Relationships portrayed in Fig. 62 indicated that a buck:doe ratio approaching 40:100 could be maintained if total annual male mortality approximated 40 percent and recruitment averaged 50 fawns:100 females.

Habitat Management for Mule Deer in Timbered Breaks Environments

Hamlin and Mackie (1989) concluded that mule deer distribution in timbered breaks was positively associated with topographic and vegetative diversity. Rough topography was of critical importance to mule deer in winter because south-facing slopes were relatively snow free, and timbered north-facing slopes provided thermal cover. Diversity of vegetation types and microclimatic conditions associated with rough topography provided forage resources and extended the period of succulent forage availability during late summer and autumn. Rough terrain also provided hiding and escape cover from natural predators and hunters. Areas with a diversity of topography and vegetation were associated with more fawning territories and consequently a higher population density.

Vegetation Management—We do not recommend large-scale vegetation manipulations (chaining, cutting, spraying, plowing, burning) that traditionally focused on increasing quantity of forage on treated areas. Our interpretation of the relative importance of habitat components is different from the "key species-key area" concept. A variety of topographic settings, vegetation types, and other habitat attributes were critical to mule deer survival. It is not possible to isolate any single habitat component that was consistently important enough to warrant direct manipulation or enhancement programs.

Mule deer in the Missouri River Breaks used all vegetation types on the study area for some purpose at some time (Hamlin and Mackie 1989). Forage production and quality across all vegetation types was determined primarily by soil type and variation in temperature and precipitation.

It is not possible to isolate any single habitat component that was consistently important enough to warrant direct manipulation or enhancement programs.
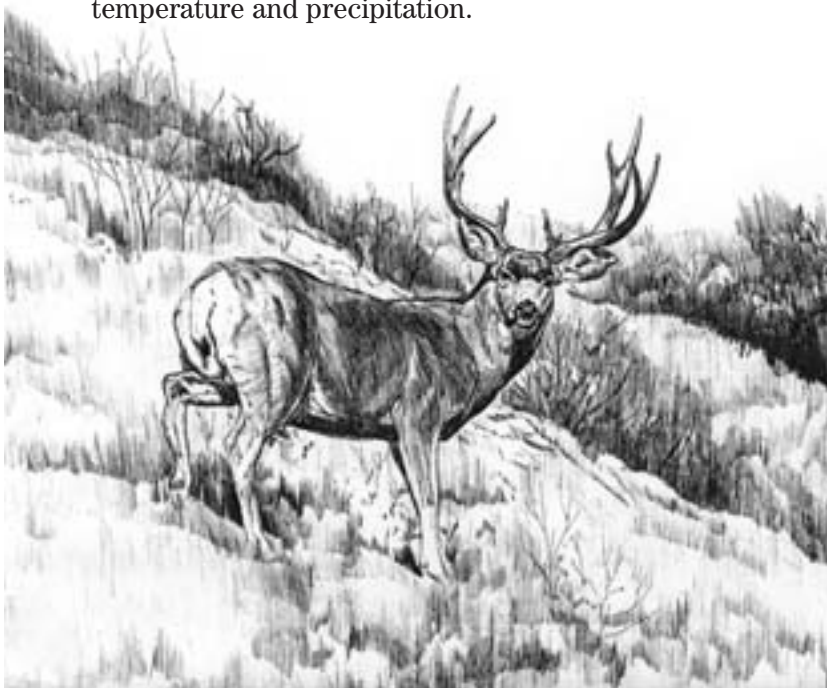
Hamlin and Mackie (1989) reported that forage quantity was not limiting during any year or season during their study. Rather, variation in forage quality (nutritional content) among years and the length of time nutritionally-adequate forage was available in any year was of major importance to mule deer physical condition and population dynamics. Density-independent, rather than density-dependent, factors exerted the primary influence on deer-nutritional relationships.

In the timbered breaks, mule deer significantly preferred Douglas fir communities during all seasons. These were relatively moist types within a drought-prone environment. Douglas fir types provided succulent forage and hiding cover during summer-autumn and thermal cover and more tolerable snow conditions during winter. All of these contribute to a positive energy balance on an annual basis.

In portions of the timbered breaks and throughout the prairie-badlands, mule deer successfully occupy many areas without Douglas fir communities. Other communities (e.g., ponderosa pine/juniper) obviously provide a similar function. Mule deer will shift their habitat use to agricultural areas when succulent forage becomes scarce in native plant communities (Knapp 1972, Griffiths 1990, and Olenicki 1993) . Agricultural crops such as alfalfa increase the time high quality forage is available to mule

...the length of time nutritionally-adequate forage was available in any year was of major importance to mule deer physical condition and population dynamics.

deer. Utilization of this resource often involves local movement of mule deer from public to private land, causing game damage problems for landowners. Where this problem is chronic, a practical application of alfalfa fields on public lands could serve as a "lure crop" and reduce deer damage to private agricultural fields and haystacks, particularly during dry years.

Livestock Grazing—Livestock grazing is the most common land use in timbered breaks environments. Relationships between livestock grazing and mule deer have been studied to a greater degree in this environment than in other parts of Montana, and they are complex. Deriving general recommendations from these studies and applying them to broad geographic areas is problematic.

Hamlin and Mackie (1989) could not detect any cause and effect differences in mule deer fawn survival or population trend between season-long and rest-rotation grazing systems during 1976-1987. Annual changes in fawn survival and recruitment that occurred under those grazing systems were apparently synchronized to broad climatic influences simultaneously affecting both areas.

Overlap in distribution, habitat use, and food habits of mule deer and cattle was minimal (Mackie 1970, Knowles 1975, Komberec 1976). Cattle primarily use the adjacent prairie grasslands, open flat ridgetops, and larger coulee bottoms. Mule deer confined their primary use to diverse, steep, timbered terrain located between areas used by cattle. Hamlin and Mackie (1989) reported that opportunity for competition was greatest in spring (April-May) when distribution and food habits exhibited the greatest overlap. Deferral of spring cattle grazing until late May would give mule deer exclusive use of sites that experience the earliest green up.

To minimize cattle use of areas important to mule deer, we recommend against development of stock water sources at the terminal portions of large ridges or on smaller ridges within the timbered breaks.

Mule Deer-Elk Interactions—Elk populations have increased significantly in portions of the timbered breaks environment. Only limited information is available to evaluate the effect of increasing elk numbers and distribution on mule deer. Hamlin and Mackie (1989) concluded that the mule deer population reached two all-time peaks despite a three-fold increase in elk numbers during the previous 20 years. A third, apparently higher peak in mule deer numbers occurred in 1993-94. It is unknown whether further increases in elk numbers will negatively influence mule deer populations.

Significant differences in habitat preferences for the two species enabled both to use the Missouri River Breaks study area with minimal conflict. Use of vegetation cover types differed during all seasons. Mule deer used areas of greater topographic relief than elk (Hamlin and Mackie 1989).

Different grazing systems and cattle stocking rates could influence habitat relationships between mule deer and elk. Campbell and Knowles (1978) indicated that elk selected rested pastures compared to grazed pastures in a rest-rotation system in the Nichols Coulee area of the Missouri River Breaks. Elk were able to make these spatial adjustments in their habitat use because of larger home ranges and greater mobility than deer. The shifting of elk away from areas used by cattle could result in greater spatial overlap between elk and mule deer, particularly if elk made greater use of rough terrain. The more limited mobility of mule deer made them more vulnerable to situations where other ungulates (cattle or elk) used their home ranges (Knowles 1975).

Access Management—Large blocks of public land occur within the timbered breaks environment, particularly along the Missouri River. Much of this expansive area is generally accessible to public hunting by a network of unimproved roads and trails. The distant location of these areas from large urban centers has not resulted in the intense hunting pressure experienced in parts of western Montana. In most areas, access to public lands in timbered breaks has been quite compatible with mule deer harvest management strategies. Hunting pressure can be expected to increase in the future on these lands as more hunters turn away from congested areas and restrictive seasons associated with the mule deer hunting experience on public lands in the western part of the state.

We recommend that travel management plans be creatively devised for important areas in the timbered breaks before problems related to heavy hunting pressure become chronic. A series of areas on public lands in eastern Montana could be strategically selected for maintaining and improving age diversity in populations of mule deer bucks. Accomplishing deer management objectives with carefully conceived hunter access plans may be preferable to making major changes in the hunting season structure once the problem becomes chronic.

Progress in maintaining and expanding hunter access to privately owned portions of the timbered breaks and prairie-badlands environments continues under MFWP Block Management and Habitat Montana programs. These efforts represent important steps in expanding hunting opportunity and help buffer the increase in hunting pressure on public land.

Mule Deer Population Ecology in Prairie-Badland Environments

Prairies represent patchy environments for mule deer. Preferred habitats occur as relatively small inclusions within large areas receiving little or no use. Therefore, population density is generally low overall. Although Wood *et al.* (1989) documented densities of 0.3-3.0 deer/km^2 on the Cherry Creek study area during 1975-1987, higher densities were recorded in small areas of preferred habitat often associated with agriculture.

Most mule deer populations in prairie-badland environments are closely associated with rugged badlands or

non-timbered breaks. Availability of badlands in units larger than 4 km^2 during winter provided minimum snow depth, shelter from wind, preferred forage, and security from predation (Dusek 1975, Geist 1981, Wood 1987). In many prairie-badlands environments, mule deer depend on native forage species during winter. Energy available in native forage is often less than daily energy requirements. Consequently, a strategy emphasizing energy conservation during severe weather and foraging during mild conditions was vital to overwinter survival. In the absence of conifer vegetation, mule deer used topographic features to help conserve energy (Wood 1988).

Winter severity and associated restrictions on habitat availability and use did not consistently limit fawn recruitment or adult survival (Wood *et al.* 1989). Rather, environmental conditions prior to and during the growing season appeared to exert primary influence on mule deer population dynamics.

During summer, springs, swales, and creek bottoms preferred by adult females during summer provided succulent forage and other resources important to fawn rearing. Annual variation in precipitation and temperature resulted in wide fluctuations in forage production and the period it remained succulent and nutritious. Wood *et al.* (1989) reported a positive correlation between fawn recruitment rate and total precipitation from July-April prior to fawning. Mackie *et al.* (1990) reported a statistically significant relationship between increasing adult density and decreased fawn recruitment the following year. However, this low fawn recruitment also occurred coincident with a decrease in precipitation from July through April.

Where prairie mule deer had yearlong access to agricultural crops, it appeared that higher population densities were sustained than in the absence of cropland. Stivers (pers. comm. 1997) recorded average densities of 8 deer/km^2 (range 3-14 deer km^2) during 1971-1996 along Sage and Indian Creeks in HD 419. Annual variation in fawn recruitment rate

Where prairie mule deer had yearlong access to agricultural crops, apparently higher population densities were sustained than in the absence of cropland.

appeared similar to other non-agricultural prairie environments.

Studies of predator-prey relationships between mule deer and coyotes, the most effective deer predator in this system, have not been conducted. Coyote densities apparently were lower in shrub-grasslands compared to timbered breaks (Pyrah 1984).

When fawn recruitment was high and hunting mortality of adult females was low, Wood *et al.* (1989) documented a 600 percent increase in mule deer population size in 8 years. When the converse was true, deer numbers declined by 70 percent in 4 years.

Mule Deer Vital Parameters and Harvest Recommendations —Variation in fawn recruitment and natural mortality of adult females in prairie-badlands environments was similar to that described for mule deer populations in timbered breaks. Consequently, the range of doe harvest rates required to stabilize adult female numbers in the prairie-badlands was also comparable (Fig. 65). Net recruitment in prairie-badlands environments was described from data spanning 12 years; mortality rates for females was based on only 5 years of data.

Unfavorable environmental conditions in prairie-badlands were associated with recruitment rates of 10-30 fawns:100 adult does and natural adult female losses between 10-12 percent. During low output phases, doe harvest rates compatible with stable numbers in the female segment varied from less than 1 to not more than 3 percent.

In most years, recruitment varied between 35-75 fawns:100 adult females while natural losses of does were 2-9 percent. Associated with this moderate output phase, female harvest rates of 4-26 percent were possible while maintaining stable numbers of does in the population.

Mule deer populations in prairie environments are capable of high output when lush growing seasons are followed by mild-moderate winters. Recruitment as high as 75-90 or more fawns:100 adult females, and negligible natural losses of adult females required doe harvest rates

Figure 65.
Recommended mule deer doe harvest rates across the span of expected variation in fawn recruitment and natural mortality of adult females in a prairie/badlands environment.

of 27-30 percent to stabilize numbers of adult females during those periods.

Annual mortality rate of adult bucks in the Cherry Creek mule deer population averaged about 60 percent, most of which resulted from hunting (Table 7). Fig. 62 correctly predicted that sex ratios of 18-20 bucks:100 does would be maintained when recruitment averaged about 55 fawns:100 females. However, very few bucks older than 3 years would be expected when mortality was ≥ 60 percent.

White-tailed Deer Population Ecology in Prairie-Agricultural Environments

Habitat for white-tailed deer in upland prairie centers on the interspersion of woody draws, dryland agricultural fields, and adjacent shrub-grass rangelands (Swenson *et al.* 1983, Dusek *et al.* 1988, Wood *et al.* 1989).

Extensive movements within large resident home ranges allowed whitetails to satisfy resource requirements. Whitetail density in prairie-agricultural environments varied from 1 to 5 deer/km^2 (Dusek *et al.* 1988, Wood *et al.* 1989). However, density is often aggregated in preferred habitats interspersed among large areas receiving little or no deer use.

Agricultural crops such as alfalfa and grain were utilized in varying amounts during all seasons. Croplands were important not only in satisfying nutritional requirements but also in creating the niche occupied by whitetails in this environment.

We speculated that whitetails usually opted for a strategy of winter survival that involved increasing energy intake by selectively foraging on agricultural crops (Dusek *et al.* 1988). Use of nutritious forage apparently compensated for much of the energy loss experienced in these open habitats during winter. Although

whitetails utilized more gentle terrain, they conserved energy during severe conditions by increased use of rough topography and woody draws similar to mule deer (Wood *et al.* 1989).

Despite their dependence on agriculture, whitetails occupying variable semi-arid environments were influenced by conditions during the growing season similar to the relationships described for mule deer in timbered breaks and prairie-badlands environments. Total precipitation received during a 10-month period (July-April) prior to fawning was positively correlated with the percentage of whitetail fawns recruited to spring populations. Consequently in populations of both species increased and decreased similarly across the span of environmental variation that occurred.

Epizootic hemorrhagic disease (EHD) occurs periodically and results in significant mortality of all sex and age classes in some whitetail populations during late summer. The disease is most common in Montana east of an approximate north-south line extending through Lewistown (Walcheck 1978, Swenson 1979, Feldner and Smith 1981). Periodic unpredictable losses of 33 percent or more of a population can occur (Swenson 1979).

Influences of coyote predation on white-tailed deer population dynamics in prairie-agricultural areas have not been studied in Montana.

White-tailed Deer Vital Parameters and Harvest Recommendations—Wood *et al.* (1989) reported fawn recruitment rates during an 11-year period for a white-tailed deer population in a prairie-agricultural environment. Only 4 years of data on mortality rates of adult females and males were available.

Low, moderate, and high output phases for prairie-agricultural whitetail populations (Fig. 66) were similar to mule deer populations occupying the prairie-badlands (Fig. 65). Whitetail recruitment rates were higher (ave. = 66±30, coef.
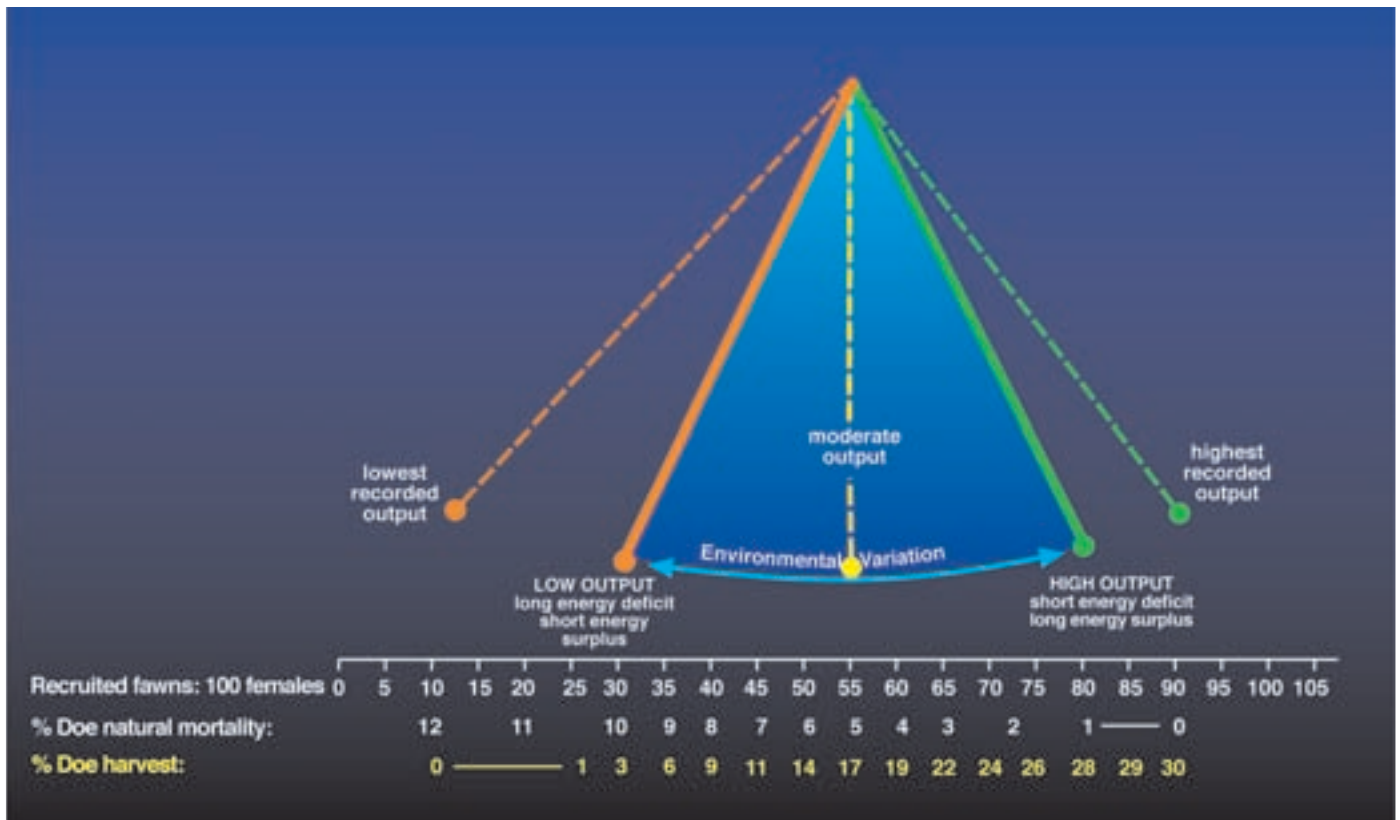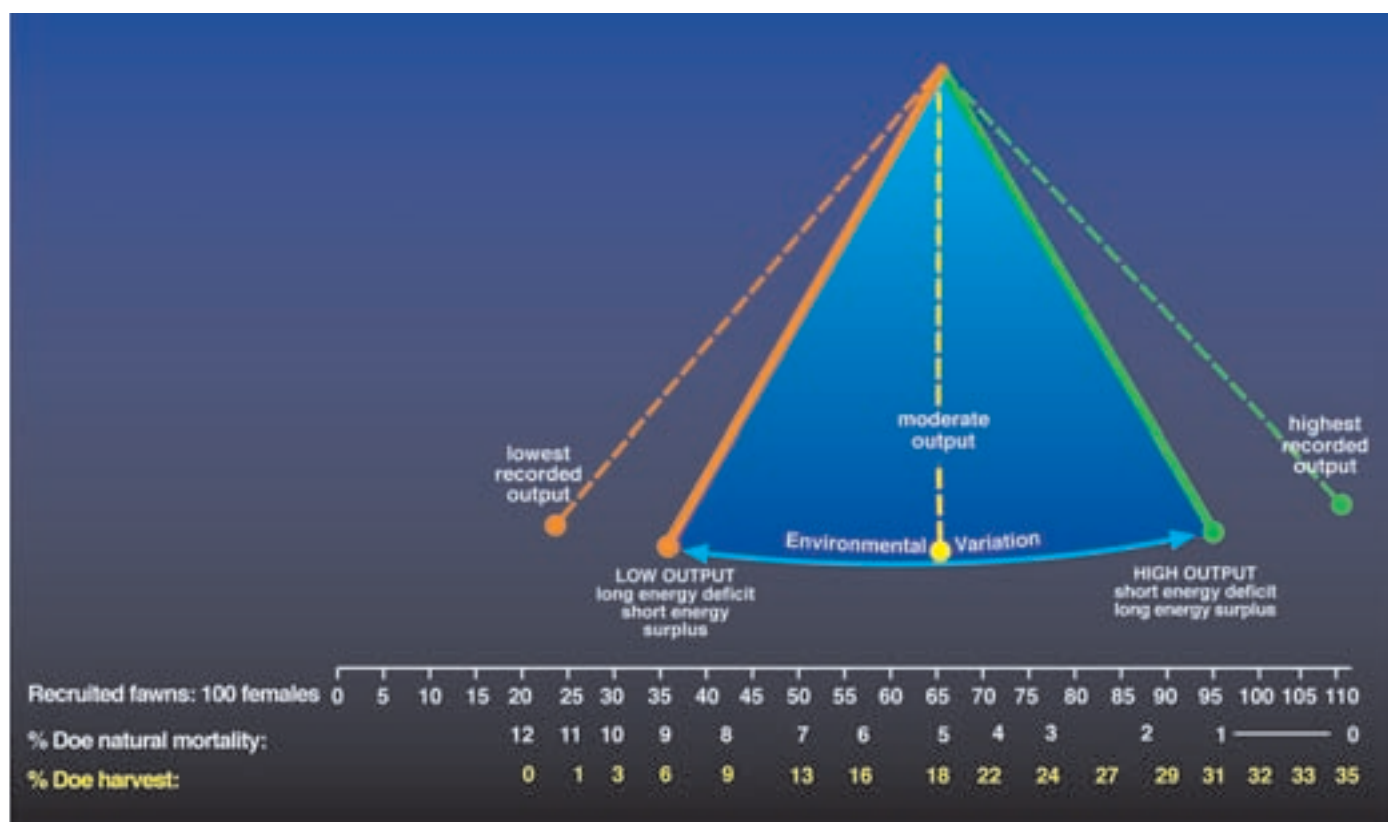

Figure 66.
Recommended white-tailed doe harvest rates across the span of expected variation in fawn recruitment and natural mortality of adult females in a prairie/agricultural environment.

var. = 45 percent) than those for mule deer (ave. = 56±24, coef. var. = 43 percent), but similarly variable (Table 4). Natural mortality rates among adult females of both species in prairie-badland and prairie-agricultural environments were similar. During a low output phase, whitetail doe harvest rates of 1-6 percent would stabilize numbers of adult females. The stabilizing harvest rate varied from 7 to 29 percent across a span of moderate output and was 29-35 percent during periods of high output.

The annual mortality rate of adult whitetail bucks was approximately 55 percent (Wood *et al.* 1989). Observed postseason buck:doe ratios averaging 28:100 could be maintained with that mortality rate because recruitment rates averaged 65 fawns:100 adult females.

Special Deer Population Management Issues in Prairie Environments

Management of white-tailed deer in prairie-agricultural environments and mule deer in prairie-badland environments constitutes a challenging "balancing act" between different land ownership concerns and changes in deer numbers on those lands. Decisive action is particular important to successful deer management. Management responsiveness begins with a well-organized monitoring system that can detect major changes in deer populations. This information must initiate an administrative process that can rapidly implement the appropriate regulation package to accomplish a distinct change in harvest rate.

Management credibility is tested by private landowner tolerance during deer population highs and by hunters and the general public during population lows. Harvest management during moderate population outputs draws far less public attention. Interest in improving management tends to focus only at the two extremes of change. However, the capability to design regulations that accomplish appropriate harvest rates during the "quiet", intervening years is

of equal importance because this is when managers have the best opportunity to bring population size closer to the goal for a particular area. Consequently, population changes experienced during ensuing decline or increase phases may be of lower magnitude and the harvest regulation changes may not be as drastic, resulting in fewer repercussions in the public arena.

Management goals for deer population size should be stratified according to land ownership. On private lands, control of deer numbers is a priority concern and requires close cooperation between wildlife managers, landowners, and hunters. A particularly liberal set of regulation packages should be focused on those areas where private land occurs in large blocks.

In general, whitetail harvest objectives on private lands should be given priority because of their integral association with agriculture. When deer populations are at moderate-high levels in eastern Montana, hunter numbers in local communities are often inadequate to meet harvest objectives. It is necessary to attract additional hunters from other parts of the state, or issue multiple licenses. To solve important and often chronic game damage situations, available hunting pressure must be directed to private lands designated as high priority. This may

Management credibility is tested by private landowner tolerance during deer population highs and by hunters and the general public during population lows.

require greater specificity in identifying where additional antlerless tags are valid. In some cases, smaller hunting units may be necessary. Entry into Block Management Programs could also be prioritized to achieve greater access in high priority game damage areas.

On large blocks of public land, a more conservative set of harvest regulations may apply. This could require greater refinement in hunting district boundaries or designated subunits within existing large hunting districts. It could also require changes in the way over-the-counter antlerless tags are issued. In the past, liberal harvest regulations designed to reduce populations on private land have been applied broadly to encompass all land ownership. Harvest pressure applied to antlerless deer on public lands competes with opportunity for controlling excessive deer numbers on private lands. Most of the time, a general either-sex license would be appropriate for both land ownerships. Additional antlerless licenses could be limited to private lands or specific areas where ownership is intermixed.

Habitat Management in Prairie-Badland and Prairie-Agricultural Environments

Habitat components of fundamental importance to mule deer in prairie badlands include rugged topography and springs, seeps, or creek bottoms that provide vegetative cover and high quality forage. White-tailed deer in prairie-agricultural environments require interspersed brushy draws and agricultural cropland. Prairie environments encompass higher percentages of private land than most mountain and timbered breaks environments. Habitat management programs and expectations for either species must be aligned to these differences in land ownership.

Agricultural croplands positively affect white-tailed deer distribution and density when fields remain small and native habitats are maintained in close proximity. There are probably many

There probably are many more whitetails in the prairies of today than during pre-settlement times when it was native rangeland.

more whitetails in the prairies of today than during pre-settlement times when it was native rangeland. Relationships between agriculture and mule deer are less clear. Most croplands occur on flat terrain that probably would receive limited use by mule deer in the absence of agriculture. Large scale elimination of shrub/grasslands may have been detrimental to mule deer in some areas directly adjacent to rough topography. Introduction of alfalfa fields in areas adjacent to rugged topography can be expected to benefit mule deer, but these situations often generate chronic deer damage complaints.

For purposes of soil stabilization, substantial areas of cropland have been converted under the Federal Conservation Reserve Program (CRP) to vegetation types including substantial amounts of alfalfa and sweet clover that appear to be preferred by deer, particularly whitetails. We speculate that CRP contributes to deer population increases in some intensively-farmed areas where it enhances habitat diversity. A possible unintended outcome has been an increase in white-tailed deer numbers in areas of private land where they are least welcome.

Protecting wooded draws, creek bottoms, and other mesic areas from heavy livestock grazing should be beneficial to both species (Kraft 1989, Wood *et al.* 1989, Jackson 1990). This would be applicable to mule deer when these areas occur within rugged topography, and for white-tailed deer when applied to mesic areas within or adjacent to agricultural croplands.

Riverbottom Agricultural Ecosystem

The riverbottom agricultural ecosystem includes irrigated and non-irrigated croplands associated with fertile valleys and bottomlands along major rivers of Montana. We delineated two environmental subcategories; plains riverbottoms and intermountain valleys. The first includes the mainstem of the

Yellowstone River and portions of its principal tributaries such as the Clark Fork, Bighorn, Tongue, and Powder Rivers. It also includes portions of the mainstem Missouri River and its tributaries wherever narrow, fertile floodplains provide a mixture of riparian forest and irrigated croplands. The regional climate prevailing over the eastern plains riverbottoms is semi-arid. Irrigated floodplains represent a veritable oasis in an otherwise dry, variable, prairie environment. Important vegetation communities include cottonwood (*Populus* sp.), green ash (*Fraxinus pennsylvanica*), willow (*Salix* sp.), shrublands, and grasslands. Crops include alfalfa, sugar beets, pinto beans, corn, and grain. Livestock grazing is prevalent.

Intermountain valley environments are found closer to the headwater basins of major river drainages in western Montana. They provide widely distributed riparian plant communities, irrigated and non-irrigated croplands, grazed areas, and urban development. Examples east of the Continental Divide include the Gallatin, Jefferson, Shields, and Paradise Valleys. The lower Flathead, Bitterroot, Clark Fork, Blackfoot, and portions of the Kootenai Valleys are examples west of the Divide. Compared to the plains riverbottoms, annual precipitation and average snowfall are greater in the intermountain valleys though deep, persistent snow cover is infrequent.

Riverbottom agricultural environments support abundant, productive white-tailed deer populations. Today, mule deer are more incidental in their occurrence or make seasonal forays into major riverbottoms. Land ownership is essentially private. Hunting access varies significantly but is generally more limited in the intermountain valleys.

White-tailed Deer Population Ecology in Plains Riverbottom Environments

Knowledge concerning the ecology of white-tailed deer in this environment is based primarily on studies along the

lower Yellowstone River (Herriges 1986, Compton 1986, Compton *et al.* 1988, Dusek *et al.* 1989). The highest deer densities recorded for either species in Montana occurred in this area. Overall white-tailed deer density on the lower Yellowstone varied between 14-27 deer/km^2 during 1981-1987 (Dusek *et al.* 1989). Densities as high as 50/km^2 were recorded on smaller sections of river bottom during years of peak populations.

Abundance of deer varied according to the characteristics of the river channel. The highest density occurred where the river channel meandered and formed bottomlands that supported large tracts of riparian forest (Boggs 1984, Compton *et al.* 1988). Lower deer densities were found along straight sections of river channel where bottomlands and riparian cover were limited.

Riparian vegetation provided cover and natural forage yearlong and was particularly important to adult females during fawning. These habitats were allocated among maternal does through territorial behavior associated with fawning. At low deer density, all females occupied optimal habitats and fawn recruitment was high. At high densities, many young does move to lower quality habitat where they lost one or both fawns. Increased social strife at high density caused more frequent aggressive encounters as evidenced by greater mobility among females. This resulted

in lower fawn survival among prime- and older-aged does (Dusek *et al.* 1989). Thus, density-dependent changes in fawn survival were caused by social behavior rather than competition for winter forage. Whitetail populations in plains riverbottom environments demonstrate resiliency to harvest exploitation because fawn recruitment rates display a compensatory response to reduction in female density.

Availability of high quality food was abundant yearlong. Irrigated crops supplemented the summer diet and may have buffered the effect of drought conditions that reduced forage quality and availability elsewhere. Whitetails consistently foraged on high-energy foods such as alfalfa, sugar beets, and grain in winter, thus avoiding significant energy deficits. Seasonal trends in their physical condition indicated that fawns and adult females maintained their body weight to late winter similar to deer supplementally fed high quality forage in penned studies.

Annual fawn mortality (ave = 50 percent) was the lowest of any deer population studied in Montana. Magnitude, timing, and cause of mortality among fawns and adults occurred in a pattern different from deer populations in other environments. Eighty-six percent of 179 documented deaths of collared deer >4 months of age occurred during September-November, 7 percent during winter, 5 percent during spring, and 2 percent during summer (Dusek *et al.* 1989). Predation and winter kill were minor causes of death among riverbottom whitetails while hunter-kill, road-kill, and periodic losses to epizootic hemorrhagic disease were important. Dusek *et al.* (1989) estimated that 26 percent and 2 percent of autumn populations were killed annually by hunting and automobile-deer collisions, respectively. Swenson (1979) estimated losses of approximately 33 percent of the whitetail population along the lower Yellowstone to EHD in the late 1970s.

White-tailed Deer Vital Parameters and Harvest Recommendations—In contrast to other deer populations in Montana, environmental variation had only minor influence on population dynamics of whitetails in riverbottom agricultural environments. Here, resources of importance to deer were comparatively more stable in their yearlong availability than in other environments. Population output phases were influenced primarily by adult female density. This important difference precluded use of a pendulum graph to describe whitetail population dynamics in this environment.

Recruitment averaged 75±20 fawns:100 adult females, the highest recorded among all deer populations studied in Montana (Table 4). Variation in the fawn recruitment rate along the lower Yellowstone (coefficient of variation =27 percent) was much lower than other deer populations east of the Continental Divide.

Mortality rates of adult females along the lower Yellowstone (Dusek *et al.* 1992) were calculated using the Micromort Software Program. Natural

mortality rates in plains riverbottom environments for females 2 years and older were somewhat higher (11-16 percent) compared to other deer populations (Table 6) and appeared to display relatively little annual variation. However, Dusek *et al.* (1992) concluded that opportunity was limited for hunting mortality to substitute for non-hunting mortality of adult females.

On the lower Yellowstone, recruitment of 50-55 fawns:100 adult females was associated with high densities of adult females. Under a prevailing natural mortality rate of 14 percent of adult females at this low output phase, a harvest of only 6 percent would keep the population from increasing. The management prescription for this area usually requires a significant harvest of females to reduce the population to a level within landowner tolerances at these high deer densities. This is particularly challenging because harvests must overcome the compensatory increases in fawn recruitment that will occur as population density is reduced. Adult female natural mortality rates could have varied from 5-14 percent depending upon the method of estimation. If the lower natural mortality estimate was most nearly correct, then a 25-28 percent hunter harvest of adult females would accomplish a decline in that segment. A 16-19 percent harvest would be required if the higher estimate of natural mortality was in effect. High levels of female harvest in this population were only accomplished by issuing each hunter multiple antlerless tags in addition to the either-sex general license. Dusek *et al.*

(1989) indicated this approach resulted in a harvest of 30-33 percent of adult females which initiated a population decline in 1984 and 1985.

If the management goal is to maintain certain whitetail populations at moderate levels in the plains riverbottom ecosystem, a sustained total annual mortality rate (harvest and natural mortality) of about 25 percent of adult females may be necessary. These rates are subject to change depending on local management goals, rates of recruitment, and natural mortality that apply to a particular whitetail population. Whitetails occupying other plains riverbottom (Allen 1968, Hamlin 1979, 1980) or intermountain valley environments with less intensive water development and less irrigated cropland may experience lower and more variable fawn recruitment rates and a lower spectrum of female harvest rates.

Buck hunting mortality rate averaged 58 ± 11 percent annually. However, a relatively high, average postseason buck:doe ratio of 25:100 was maintained because fawn recruitment was high and stable.

For general reference, Table 9 provides the estimated harvest rates achieved for each sex and age class and the corresponding effects on population trend during a 6-year period on the lower Yellowstone (Dusek *et al.* 1989).

Essentially no data have been collected on recruitment, natural mortality rates, or population size for whitetails in intermountain valley environments. We speculate that dynamics of these populations may be similar to whitetails

In contrast to other deer populations in Montana, environmental variation had only minor influence on population dynamics of whitetails in riverbottom agricultural environments.

Table 9.
Harvest rates by sex and age class and their general effects on white-tailed deer population trend on the lower Yellowstone (after Dusek et al. *1989).*

Percent Harvest by Sex and Age Class					
Year	Total Population	Adult Females	Adult Bucks	Fawns	Effect on Population Trend
1980	13	11	38	3	Increase
1981	14	6	60	5	Increase
1982	25	14	68	10	Increase
1983	32	26	69	14	Stable
1984	35	30	53	17	Decline
1985	34	33	57	22	Decline

in plains river bottoms, although effects of winter severity may be somewhat more influential and require more conservative harvest rates.

Whitetails in riverbottom-agricultural areas have the greatest potential for causing crop damage because of high deer density and productivity per unit of occupied habitat. Hunter access to private land is of critical importance to whitetail harvest management in these areas. Compared to other environments, more consistent and intense hunting pressure must be focused on riverbottom whitetails to keep them within levels tolerable to landowners. Evenly distributed, dependable, long term hunter access agreements are a key element in consistently directing hunting pressure to these lands. These areas require priority status when implementing hunter access programs. Alternatively, multiple licenses issued to limited numbers of hunters that can gain access to private lands may also be used to harvest these populations.

Habitat Management for White-tailed Deer in Riverbottom-Agricultural Ecosystems

In plains riverbottoms and intermountain valleys, white-tailed deer rely on the interspersion of riparian vegetation and agricultural croplands for all their resource requirements. Following are our primary recommendations:

• Maintenance of successional relationships in riparian vegetation communities is fundamentally related to periodic flooding which also causes bank erosion and deposition of sediments to form bottomlands. If flooding is minimized by water impoundments or diversions, bank cutting is reduced and successionally advanced plant communities (grasslands) become more common (Boggs 1984). White-tailed deer selected for mid-late successional communities such as mature cottonwood, shrub, green ash, and mature willow with tall dense cover (Herriges 1986). In the absence of periodic flooding, there is minimal replacement of these plant communities in the riparian system.

• Large scale land clearing, burning, or logging of cottonwood stands removes existing riparian forests and rapidly advances succession toward grasslands which could result in reduced white-tailed deer densities.

• The linear relationship between deer density and amount of riparian cover (Compton *et al.* 1988) may provide a useful tool for indexing relative abundance of white-tailed deer along major rivers in the agricultural areas of Montana.

• Maintenance of large tracts of dense, woody, riparian vegetation provides important security cover for white-tailed deer occupying areas of intense human activity (Vogel 1983, Herriges 1986).

• Housing developments in the western intermountain valleys were least compatible with use by white-tailed deer when housing was evenly distributed. Vogel (1989) recommended a strategy of clustering housing density on or near already developing areas, especially those of little value to agriculture or wildlife, rather than develop new areas.

• In areas where chronic problems occur with high density white-tailed deer populations, elimination of riparian cover in combination with heavy hunter harvest or other types of removal may offer the only long-term solution.

• White-tailed deer distribution was negatively influenced by the presence of cattle on the river bottom (Compton *et al.* 1988). When cattle were introduced, deer moved immediately to the nearest cattle-free area. Deer resumed use of the area when cattle were removed. This suggested that, as observed for elk and other cervids (Lonner and Mackie 1983), avoidance of cattle may reflect social intolerance rather than forage competition.

• Alfalfa fields associated with riparian cover were used to a greater extent than fields without nearby cover. Deer use of alfalfa fields during summer increased with distance from human settlement, amounts of adjacent cropland other than alfalfa, and amount of nearby

breaks topography (Rausher 1995). Densities of 19 deer/hectare/day for 30 days or more were required for deer foraging to significantly reduce alfalfa yields during the growing season. These densities were seldom reached along the lower Yellowstone River (Herriges 1986, Rauscher 1995).

• White-tailed deer use of sugar beets and winter wheat did not appear to be heavy enough to cause damage of economic significance (Herriges 1986). Beet fields did not receive heavy use during the summer growing season. Large numbers of deer used early green up in some winter wheat fields, though the large size of these fields probably reduced potential for substantial economic damage.

• Development of small fields of alfalfa or grain in areas of riparian cover on state-owned lands could reduce deer use of adjacent private lands. Only two cuttings of alfalfa should be harvested so stands are maintained in vigorous condition (Herriges 1986).

Future Directions in Deer Management

The impetus for progressive change often occurs in the aftermath of declines in abundance of an important resource. Response to declining deer populations in Montana during the mid-1970s emphasized the need for ecologically-based knowledge of deer populations and their habitats. Montana FWP initiated a series of long-term studies that ultimately resulted in the description of habitat relationships and population dynamics summarized in this document. The decline in deer populations during the mid-1990s has recently provided the opportunity to merge that knowledge of deer population biology with a more innovative management process.

Adaptive Deer Management

The concept of adaptive management of natural resources was initially defined almost 20 years ago by Walters and Hilborn (1978). More recent applications have been described by Walters (1986), Johnson *et al.* (1993), and Williams and Johnson (1995). It is a process that functionally integrates the basic components of management to positively influence administrative decisions concerning harvest regulations. The primary outcome is to recommend harvest management practices that optimize hunter harvests of populations occupying dynamic ecological and social environments.

Our understanding of the relationships between deer population dynamics and hunter harvest still has serious limitations. This uncertainty results in differences of opinion concerning harvest management within MFWP and the general public. Walters (1986) concluded that we learn about responses of natural populations to harvest strategies mainly through experience. This can only be accomplished if management is conducted within the context of systematically measuring the effects of harvest regulations and other important environmental factors on deer populations. This measurement and its feedback to management represents the essence of adaptive deer management and sets it apart from traditional approaches.

MFWP officially began development of an Adaptive Deer Management (ADM) program in 1996. The basic components that are linked together in this process include specific deer population objectives, distinct sets of harvest regulations, a monitoring program, and alternative models of population dynamics. The following comments are preliminary because there is much to be learned about application of these concepts to management of deer in Montana.

Deer Population Objectives

Deer population objectives are an integral component of ADM because they influence the outcome of the entire management program. Specific objectives for population and harvest

management are required to define direction and measure progress over time. However, determining objectives is often the most difficult task. We recommend that the ecological spectrum of deer population dynamics described in this document should frame the key elements of management goals, objectives, and strategies. Differences in biology and socioeconomic concerns warrant separate management programs specific sets of objectives for each species. This approach would provide greater management resolution and responsiveness.

Specific objectives should be directed toward important, individual populations or groups of populations that occupy a similar ecological system. Objectives focusing on management of the total population in a particular area should clearly describe the desired numerical size and acceptable limits of fluctuation based on biological and social (landowner and sportsman) considerations.

Earlier in this document, we described phases of variation in vital population parameters and corresponding harvest rates that would decrease, stabilize, or increase population size. Objectives should include quantified threshold levels in these parameters or "triggers" that cause a change to a more conservative or liberal set of regulations. Parameter levels used in the objectives would apply to those deer populations that are censused in the monitoring program.

Objectives for increasing buck availability and age diversity could be described in a similar manner. However, descriptive parameters and triggering mechanisms might then include numbers of bucks and buck:doe ratios in post season populations as well as age structure and antler size in the harvest.

Harvest Regulations

We do not describe specific harvest regulations because a variety of social and economic considerations exert influence on local and regional deer management

strategies. Variation in habitat security, proximity to urban areas, land ownership, and hunter access can create broad differences in the rate of harvest achieved by a particular regulation. Regional managers can integrate the population parameters and harvest rates summarized in this document with these other considerations to tailor regulations appropriate to their areas.

Harvest regulations can be designed to fit each species and ecological setting. Including a restrictive, moderate, and liberal regulation will provide an appropriate array of harvest rates. The intent is to achieve the proper harvest according to the status of the population and its current position relative to management objectives. When a change in harvest strategy is warranted, the adjustment in harvest rate should be large enough to detect a population response through the monitoring program. Regulations that are easily understood by the hunter will be most acceptable, and they should be easily enforced. However, goals to both simplify regulations and increase the diversity of buck hunting opportunity may conflict. The targeted rate of harvest to be achieved by a particular regulation should be specific to adult females and/or adult bucks, depending on population management objectives.

In variable environments occupied by deer in Montana, populations may not respond in a predictable or desired direction even when a prescribed harvest rate is achieved. In these situations, knowledge of deer population dynamics and effectiveness of harvest regulations would be significantly increased if hunting seasons were evaluated as management experiments. Use of treatment and control areas within the same ecological system could potentially sort out effects of harvest from environmental variation on trends in population size.

Different sets of harvest regulations should be applied to mule deer populations occupying mountain and prairie ecosystems. It appeared that dynamics of populations in the timbered breaks environment were

We recommend that the ecological spectrum of deer population dynamics described in ths document should frame the key elements of management goals, objectives, and strategies.

generally similar to populations in the prairie-badlands and may not warrant separate regulations. However, spatial and temporal variation in population dynamics may require that more than one component of the regulation package could be applied to parts of this vast area within the same year. White-tailed deer populations occupying northwest montane forest, prairie-agricultural, and river bottom-agricultural environments may require three distinct sets of regulations. Additional regulations may result from new information collected on deer populations in other ecological settings or as required by differences in land ownership, game damage, or hunting pressure.

Deer Population Monitoring

A clearly focused monitoring program is essential to implementing innovative approaches in deer management. Informed decisions must be based on systematic and consistent data on population status and trend, achieved harvest rates, and how these relate to important environmental factors. As a starting point, we recommend a statewide network of census areas for each species of deer distributed across important ecological categories described in this

A clearly focused monitoring program is essential to implementing innovative approaches in deer management.

document. For mule deer, these include mountain-foothill, northwest montane, timbered breaks, and prairie-badlands. Census areas for white-tailed deer should be distributed within mountain-foothill, northwest montane, riverbottom-agricultural, and prairie-agricultural environments. Although separate sets of regulations may not be necessary for each of these combinations, we believe that some monitoring sites should occur in all types to account for spatial and temporal differences in population trends as well as socioeconomic considerations. Discussions with local biologists are required before the number and location of census areas are determined. Funding and data collection on these selected census areas would receive priority over other deer trend areas.

Subsequent discussions of monitoring techniques will be confined to environments where it is feasible to conduct aerial surveys with helicopters or Piper Supercubs. Fortunately this includes about 75 percent of the land area in Montana. Other ground-based techniques such as camera surveys (Dusek and Mace 1991, Sime 1996) may be appropriate in densely timbered habitats. Specific recommendations include:

• Where possible, "full coverage" flights over the census area be conducted during each aerial survey (Mackie *et al.* 1981). Consistency in this effort will maximize the number of deer counted in relation to the total number present on the area. Using these methods, consistent percentages of deer have been observed in various environments with helicopters and Supercubs (Table 10). These aerial observability indices could be used to convert total numbers of deer counted to an estimate of population size. Each census area should be flown twice each year, post-hunting season and spring.

• Primary population parameters measured in post-season census are total numbers, fawn:doe and buck:doe ratios, and antler point classes. Post-season flights should occur between December 1 and January 15 for mule deer and no later than January 1 for whitetails because of earlier antler shedding.

Table 10.
Aerial observability indexes measured from samples of marked deer in various environments in Montana.

Environmental Type	Study Area	Aircraft	% Observability Index (x̄ ±1sd)	Number of Surveys
Mule Deer - Post Season Surveys				
Mountain-foothills (timbered)	Bridger Mts. (PHU1)	Jet Ranger, Bell 47G	46±13	7
Mountain-foothills (shrub/grassland)	Bridgers Mts. (PHU4)	Jet Ranger, Bell 47G	41±12	5
Timbered breaks	Missouri River Breaks	Bell Soloy, Bell 47G	75±7	10
Prairie-badlands	Cherry Creek	Supercub	70±5	4
Mule Deer - Spring Surveys				
Mountain-foothills (timbered)	Bridgers Mts. (PHU1)	Jet Ranger, Bell 47G	57±7	10
Mountain-foothills (shrub/grassland)	Bridgers Mts. (PHU4)	Jet Ranger, Bell 47G	68±12	9
Mountain-foothills	Rocky Mt. Front	Bell 47G	57±7	5
Timbered breaks	Missouri River Breaks	Bell 47G	74	2
Timbered breaks	Missouri River Breaks	Supercub	68±5	7
Timbered breaks (with agriculture)	Lower Stillwater	Bell 47G	58±11	4
Prairie-badlands	Cherry Creek	Supercub	65±6	5
Prairie-badlands	Hammond Area	Supercub	76±5	6
White-tailed Deer - Post Season Surveys				
Prairie-agricultural	Cherry Cr.	Supercub	51±1	3
White-tailed Deer - Spring Surveys				
Prairie-agricultural	Cherry Cr.	Supercub	57±6	4
Plains riverbottom	Lower Yellowstone-Elk Island	Supercub	25±2	15
Plains riverbottom	Lower Yellowstone-Intake	Supercub	35±3	15

• Primary parameters measured during spring census are total numbers and fawn:adult ratios. Census flights no later than 2 weeks after the beginning of spring greenup will optimize observability. This period varies from year to year depending on plant phenology but usually occurs between March 15 and April 30.

During both census periods, deer observations recorded by social group size and composition will provide the greatest amount of information. Location of deer groups can be recorded by drainage name and elevation or global positioning system (GPS) methods. Classification of sex and age classes is most efficient when the pilot presents the observer with a low-level "broad-side" view of all members of the group. After a group of deer is classified and tabulated,

the aircraft should turn the group back toward the area already counted; this is most important on areas with high deer density. Survey time and weather conditions such as cloud cover, wind, relative snow depth and coverage, and temperature should be recorded as well as deer behavior relative to use of open or timbered sites. Ideally, surveys are conducted with either total snow cover or total bare ground as opposed to patchy snow conditions. However, completing the census is most important, regardless of snow conditions. More details on aerial survey methodology are provided in Unsworth *et al.* (1994).

Selecting the size and boundaries of census areas is critical in minimizing ingress and egress of deer during and between sampling periods. This will

ensure that numbers of deer counted over time will reflect actual changes in population size. Populations that have been the subject of telemetry studies of seasonal and yearlong distribution should receive first priority in selecting census areas.

An ecologically complete unit of winter range should represent the census area in mountain habitats with migratory deer. Use of helicopters for census flights will enhance observability in rugged, partially timbered terrain and offer greater observer efficiency at high deer density. Upper and lower elevational boundaries within which the census is conducted will vary from year to year depending on snow depth and deer distribution. During each census we recommend that aerial coverage extend or adjust to "run out" of deer at both high and low elevations. This will account for differences in distribution between years and between bucks and does. Lateral boundaries to the census unit should represent areas that are essentially devoid of deer in winter and represent discontinuities between winter range units. Size of the census area may vary from 25-125 km^2. Because deer on mountain-foothill winter ranges usually occur at high density, sample size will almost always exceed minimal requirements (>100 females and associated bucks and fawns). Virtually all of our experience in aerial census on mountain-foothill winter ranges is with mule deer, so modifications in approach may be necessary for white-tailed deer.

Deer in prairie or timbered breaks environments primarily display resident movement patterns and are distributed at relatively low density across large expanses of habitat. Surveys can be efficiently conducted with a Piper Supercub, although a helicopter would enhance classification of bucks in timbered breaks. It is important to include a large piece of rugged terrain including springs, seeps and other moist sites in the central portion of the census area. The perimeter should be situated in relatively flat terrain with some creek bottoms that are used only

Selecting the size and boundaries of census areas is critical in minimizing ingress and egress of deer during and between sampling periods.

during peak populations. This also will help minimize movement of deer in and out of the census area. This arrangement will provide improved ability to detect population increases and decreases based on differential use of these flatter areas. Inclusion of only rugged terrain in the census area may indicate changes in population size of a much smaller magnitude than across the broader area. The census area should include a minimum of 100 adult females during population lows. This may require an area of up to 250 km^2. The increased knowledge of deer use gained by recording locations of deer groups during flights can enable a large census area to later be reduced in size without losing past years' information. However, if a census area is found to be too small and must be expanded, the end result is equivalent to starting over.

Supercub surveys have been demonstrated to be effective in estimating trends in population size and composition for white-tailed deer in the riverbottom-agricultural environment (Dusek *et al.* 1989). Habitats are essentially linear and easy to define along major river valleys. Because deer density is exceptionally high and often associated with dense riparian cover, a linear census area along approximately 25 km of river channel should be adequate. Highest deer densities are often associated with meanders in the river channel and would constitute the core of the census area. End points can be selected along straight sections of river channel where riparian cover and deer habitat diminish.

Complete snow cover will optimize survey conditions during the post-season census by maximizing the background contrast of deer located in riparian cover. We recommend partitioning the search effort according to cover density. Large pieces of riparian forest are systematically searched before moving to the next cover piece. Deer in agricultural fields are easily observed but have a greater tendency to run for cover when hazed by the aircraft. They should be turned toward cover patches already surveyed. Reliable classification of whitetail fawns will require practice.

Census flights conducted during morning and evening hours will coincide with periods when deer are most active. Spring census flights should focus on the early spring greenup when the highest proportion of deer may be using agricultural fields.

White-tailed deer census areas in prairie-agricultural environments should approximate 200-250 km^2 in size. A relatively high density of wooded cover patches in association with agriculture should occur in the central portion of the census area. Perimeter boundaries can occur in flat expanses of agricultural croplands with limited cover patches. Techniques for conducting aerial surveys are similar to those described above.

Other important components in the monitoring program for both species include the Statewide Hunter and Harvest Survey and local check stations. Both sources provide important information concerning trends in hunter effort, percent success, the magnitude of harvest achieved under different regulations, and whether harvest objectives are met. Detailed data on specific deer populations can be collected at check stations. Rates of female harvest achieved by particular

regulations are poorly understood. By connecting a check station effort with a priority census area, numbers of females harvested from the censused population could be more accurately estimated. Sex specific rates of harvest could also be estimated by employing samples of radio-collared deer in priority populations.

Alternative Models of Population Dynamics

Population modeling is a tool to increase our understanding of how and why populations change. Recent advances in modeling capabilities make it possible to more accurately describe the dynamic changes that wildlife populations experience in variable environments (Lubow 1995, Lubow *et al.* 1996). When a feedback loop is established between monitoring and modeling, more responsive management can be advanced. Modeling assists in deciding which harvest management option is appropriate for the current population status. Monitoring the managed populations measures the outcome of that decision. We caution that modeling can be ineffective in its application

to management when it substitutes for monitoring actual changes in real populations.

Models not only describe the factor interactions that affect population size and composition, they can include different assumptions about additive or compensatory effects of hunting mortality. Competing models are constructed using these different assumptions to test an array of hunting season regulations. Each model is initiated with accurate data describing the current status of representative populations and conditions of importance in the environment. In each year (t), the modeling exercise identifies a specific hunting regulation which optimizes harvest opportunity in relation to management goals while minimizing negative effects on the population in year t + 1. A hunting regulation is selected through the modeling process and then applied to actual populations that fit the ecological parameters upon which the model was designed.

After the hunting season, aerial monitoring of deer populations will provide information to compare the status of the population in year t + 1 with the predicted outcome of the various models. The model that did the best job of predicting the observed response by the actual population in year t + 1 is given more weight in the decision-making process for prescribing an optimal regulation in the next year (t + 2).

Over time, repetition of this modeling-monitoring feedback loop will improve management performance by reducing the amount of uncertainty in our knowledge concerning the effects of harvest on population dynamics. This will enhance our ability to detect and respond to significant changes in deer populations and more closely meet objectives for population size and composition. With this approach, MFWP can move forward with an innovative and progressive deer management program to meet the challenges of the twenty-first century.

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Appendix
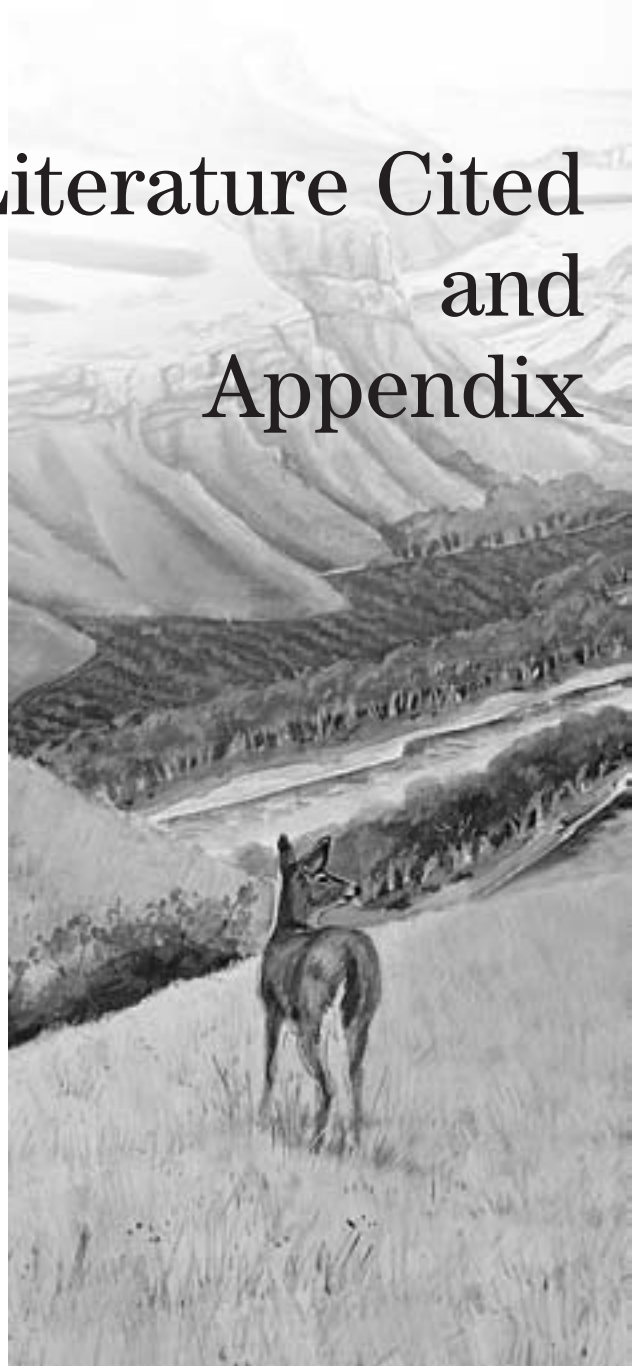
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Appendix

A List of Publications Resulting from Statewide Deer Research Studies

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